

## THE FUNCTIONAL MORPHOLOGY AND EVOLUTION OF RECENT LIMOPSIDAE (BIVALVIA, ARCOIDEA)

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### ABSTRACT

The bivalve family Limopsidae is divided into thirteen morphological classes which have not previously been recognized. These classes are defined from both shell and anatomical features. Of the former the most relevant are the degree of anterior reduction, tumidity, periostracal bristles, hinge and ligament, and of the latter the pedal, byssal and gill axis musculature. One of the most significant morphological observations is the recognition of four ligament types within the family. The morphological classes are sorted into three major functional groups—Limopsiform, Glycymeriform and Abyssate Burrowing.

The Limopsiform group contains eight of the morphological classes; in general these are semi-infaunal with degrees of endobyssate and epibyssate attachments. There are three components: 1. Ploughing. Mobile crawlers through soft substrates or over hard substrates rarely employing a byssus. 2. Endobyssate. Less mobile, generally infaunal employing a multiple-stranded byssus. 3. Epibyssate. Epifaunal with a well-adapted byssus of multiple strap-like threads.

The Glycymeriform group contains two classes which show a marked convergence with the Glycymerididae and are poor shallow burrowers: 1. A ribbed sculptured class with a wide Recent distribution. 2. A finely decussate sculptured class with a restricted range in southeast Australia.

The Abyssate Burrowing group contains three classes which may not be closely related, yet do have an antipodean bias in their distribution. Two classes are limited to southeast Australia and contain small species with some affinities with the Glycymeriform group. These are argued to be poor burrowers in sands and gravels. The third class is endemic to Antarctica and is hypothesized to contain shallow burrowers living in muddy substrates.

The evolutionary history of the Limopsidae indicates an early Cretaceous semi-infaunal origin with rapid radiation into the Limopsiform classes by the late Cretaceous. There was little functional radiation within the Limopsiform group after the Cretaceous, but there must have been a subsequent parallel morphological radiation giving rise to those species with the more advanced ligament structure. An early offshoot of this semi-infaunal group was the Glycymeriform line which appeared in the middle Cretaceous. The Glycymeriform and the Abyssate Burrowing groups, excluding the Antarctic one, had a Mid-Cenozoic radiation in the antipodean provinces, but declined in the northern hemisphere. The Antarctic class is apparently recent in origin and, significantly, possess the most advanced ligament form.

The extent of the radiation is compared with that of other byssate and burrowing arcoids and, although it is considered to be relatively wide functionally, it is not so morphologically, nor are the species diversity and distribution comparable.

A preliminary analysis suggests that the growth and morphological features of the limopsid ligament prevented radiation into the anteriorly reduced byssate forms in all except the most minute species, and that the same ligament could also not be adapted to achieve enough strength to allow radiation into the burrowing habit. The family as a whole, therefore, remained semi-infaunal. However, semi-infaunal bivalves had already been largely excluded by advanced burrowing heterodonts and consequently the limopsids were restricted to environments where competition was less extreme, e.g. the deep sea.

### INTRODUCTION

The Limopsidae are a small family of arcoid bivalves which because of their generally deep water distribution have received little attention. The affinities of the family are with the

Glycymerididae and Philobryidae, although the exact nature of the relationship is not agreed upon (Tevesz, 1977; Nicol, 1950).

The Limopsidae and Philobryidae are of considerable interest with regard to the adaptive radiation of the Arcoidea. They represent

the only extant forms which lack the typical chevron (duplivincular) ligament. They also possess compressed, rounded or oval shells which contrast markedly with the quadrate shells of the Arcacea. Thomas (1976) outlined the adaptive limitations of the duplivincular ligament, but it is apparent that in terms of species diversity, habitat range and geographical range the Limopsidae and Philobryidae are even more restricted.

By examining both the functional morphology and evolution of the oldest family, the Limopsidae, this paper aims to develop an hypothesis to explain at least in part why there are such restrictions.

### MATERIALS AND METHODS

Previous studies on limopsids have on the whole not taken into account the variability of shell form which arises through ontogeny or ecological factors (Dell, 1964; Knudsen, 1967, 1970; Oliver & Allen, 1980b). This has led to the erection of an unnecessary number of species and genera. For this reason it is not possible to discuss morphology or radiation using current systematic groupings. Ninety percent of the known Recent species have been examined in this study. Of the fifty species, eighteen were obtained with intact soft parts. Observations based on them have been used to construct a revised classification. Due to nomenclatural problems, all species have been placed in *Limopsis sensu lato*. The diagnoses of these morphological classes are presented in the Appendix which provides notes on habitat, depth range, geographical range and species included in each class. Throughout the text the morphological classes are referred to numerically: M.C. I to M.C. XIII. Note that the figures are in two series: Figs. 1 to 12, and App.[endix] Figs. 1 to 27.

### KEY TO ABBREVIATIONS OF INSTITUTIONS FROM WHICH FIGURED SPECIMENS WERE OBTAINED

AMS	Australian Museum, Sydney
BMNH	British Museum (Natural History), London
IRSNB	Institut Royal des Sciences Naturelles de Belgique, Brussels
MCZ	Museum of Comparative Zoology, Harvard University

MNHNP	Muséum National d'Histoire Naturelle, Paris
NM	Natal Museum, Pietermaritzburg
NMW	National Museum of Wales, Cardiff
NSMT	National Science Museum, Tokyo
RSM	Royal Scottish Museum, Edinburgh
SAM	South Australian Museum, Adelaide
USNM	United States National Museum, Washington, D.C.

### FUNCTIONAL MORPHOLOGY

Studies on the morphology of limopsids are very few. Pelseneer (1888) described the morphology of *Limopsis cancellata* (Reeve, 1843) and Burne (1920) did likewise with *L. marionensis* Smith (1885). Purchon (1957) and Dinamani (1967) described the anatomy of the stomach of *L. vaginata* Dall (1891) and *L. belcheri* (Adams & Reeve, 1850) respectively. Little functional interpretation, if any, was made in these studies. Jeffreys (1864) observed living *L. aurita* (Brocchi, 1814) and noted its ability to crawl on a smooth surface and to produce a byssus consisting of a single fine thread. Atkins (1951) noted that the ciliary currents are like those of *Glycymeris glycymeris* and *Arca tetragona* (Atkins, 1936).

Tevesz (1977) studied both the Philobryidae and Limopsidae, basing his conclusions primarily on observations made on two live Australian species, *Limopsis loringi* Angas (1873) and *L. soboles* (Iredale, 1931). Tevesz concluded that in general limopsids are convergent with the Glycymerididae, being poor shallow burrowers with an endobysate attachment. Tevesz, however, also noted that *L. antillensis* Dall (1881) is convergent with the philobryid genus *Cratis* and that philobryids are generally epibysate.

Oliver (1978) and Oliver & Allen (1980b) examined the functional morphology of the deep water Atlantic species with special reference to adaptations for this habitat. They noted a larger variety of habits than was suggested by Tevesz's study. Examination of live *L. aurita* showed that this species typically ploughs through the surface of soft sediments, remaining in a vertical position in muds but falling onto one valve in sands. It was also observed to crawl over gravels and was able to suspend itself by its byssus from larger stones or the sides of the aquarium. The large abyssal species *Limopsis tenella* Jeffreys (1876) (= *pelagica* Smith, 1885) was also suspected to be a ploughing form, but from the distribution



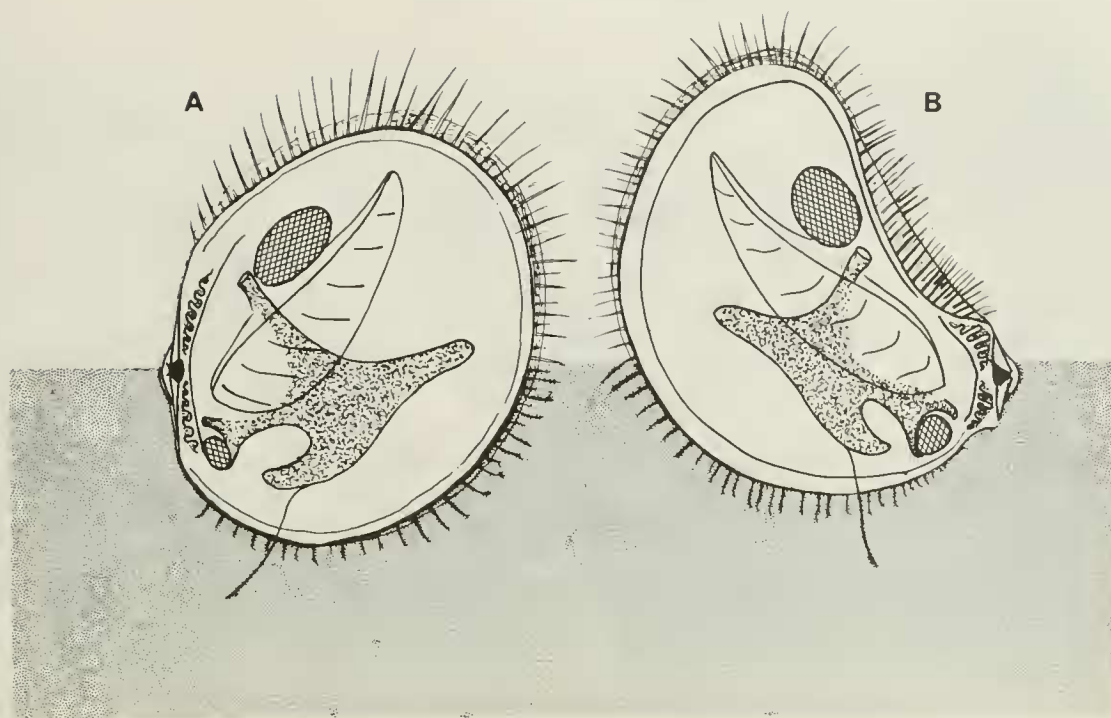


FIG. 1. Reconstructions of life positions. A. *Limopsis marionensis* (M.C. I). B. *L. vaginata* (M.C. III).

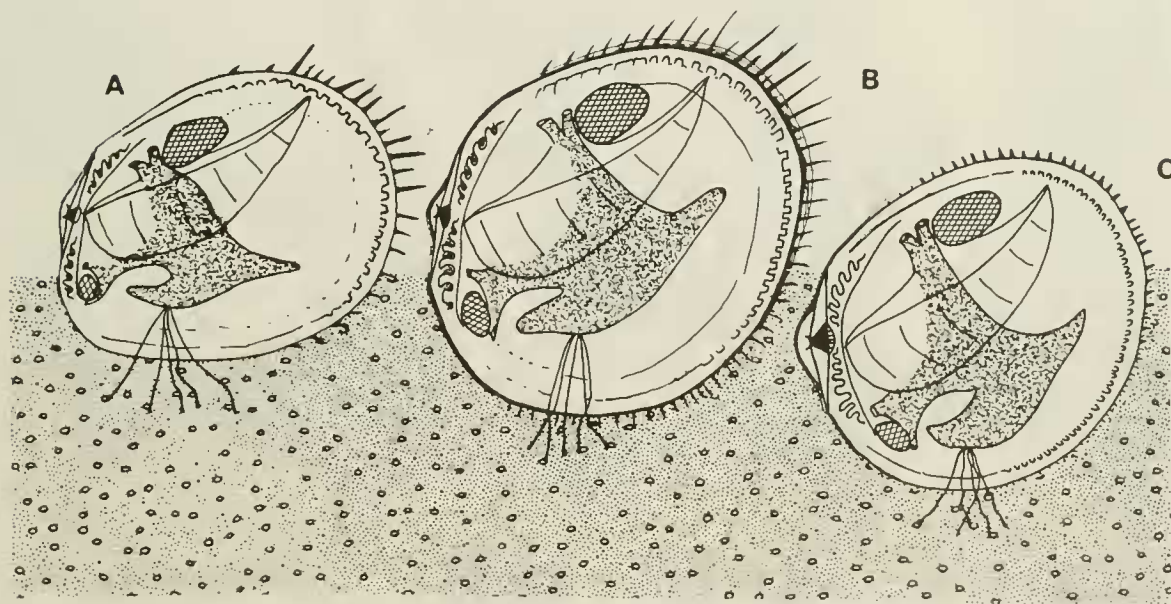


FIG. 2. Reconstructions of life positions of species in M.C. V. A. *Limopsis affinis*. B. *L. diegensis*. C. *L. oblonga*.

and size of some of the shell epifauna it was further concluded that much of its life must be spent lying on one valve. The byssus was rarely observed in *L. tenella*. A much smaller species, *L. cristata* Jeffreys (1876) (including *L. affinis* Verrill, 1885), was shown to be more infaunal, with a multiple, but finely threaded byssus. *L. minuta* (Philippi, 1836) was suspected to be, to a great extent, epibyssate.

The morphological variety exhibited in the thirteen classes is greater than any suggested

by previous studies. This variety is, however, expressed in relatively minor differences of shell and anatomical detail. Functionally significant shell characters are the outline, tumidity, anterior reduction, marginal crenulations and hinge strength. Anatomical characters of importance are the foot, byssus apparatus, gill axis musculature and mantle margin musculature. Using these characters it is possible to recognize three major groups containing morphological classes with a high degree of

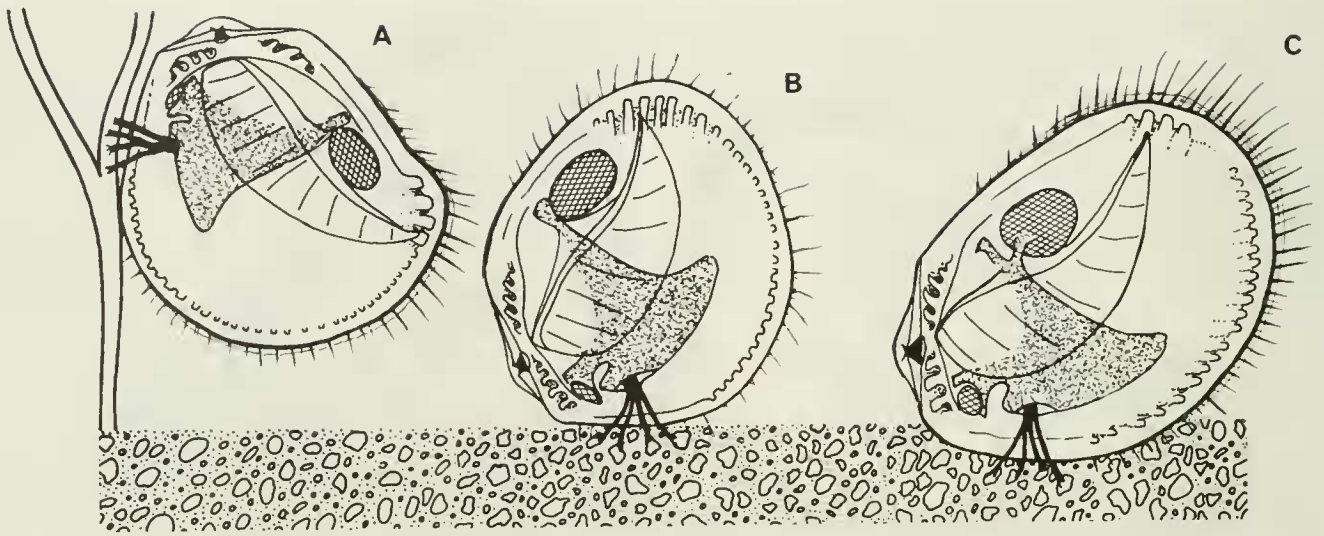


FIG. 3. Reconstructions of life positions. A. *Limopsis natalis* (M.C. VIII). B. *L. elachista* (M.C. VIII). C. *L. minuta* (M.C. VII).

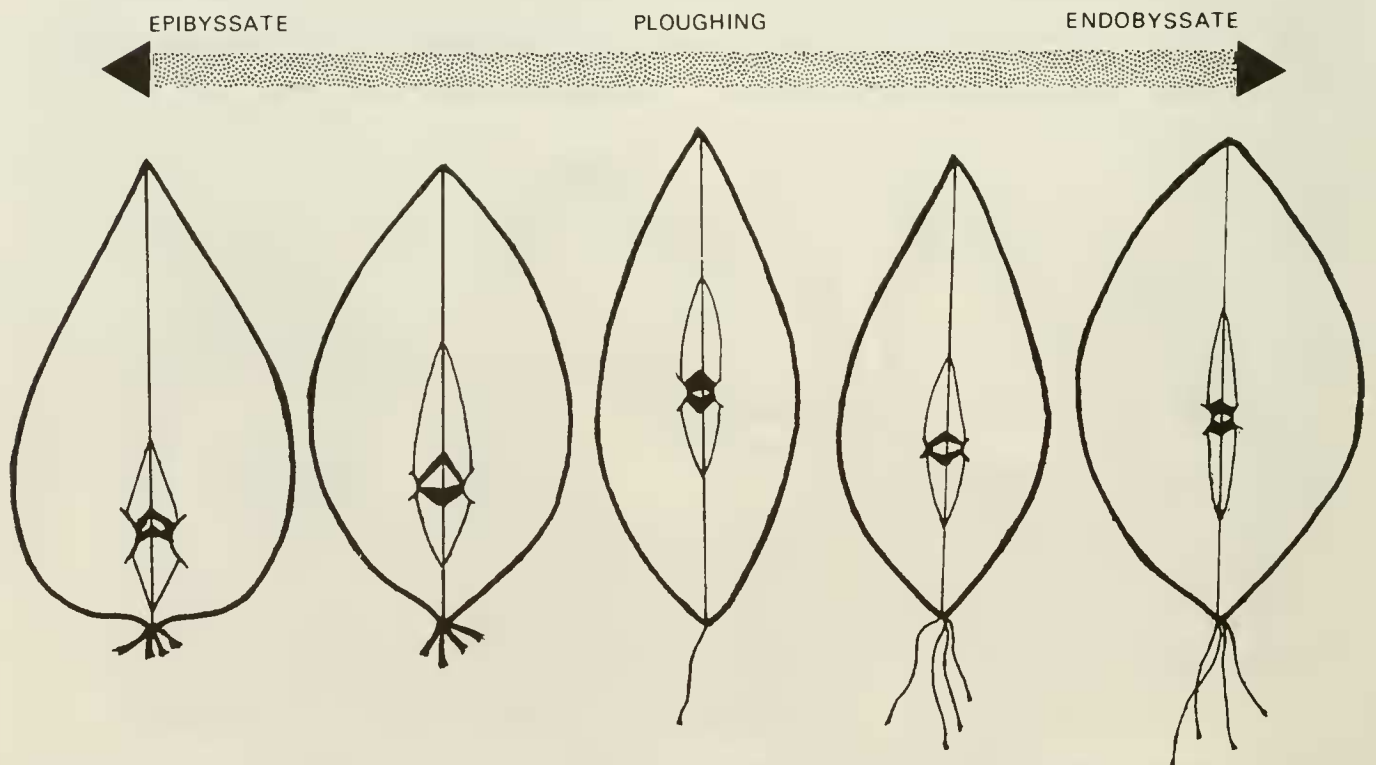


FIG. 4. Tumidity and anterior reduction in relation to limopoid habits.

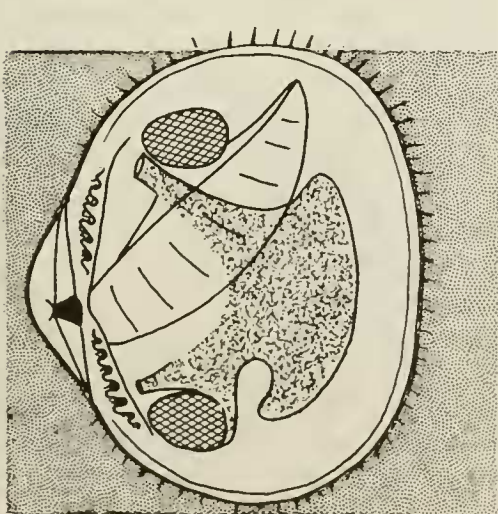
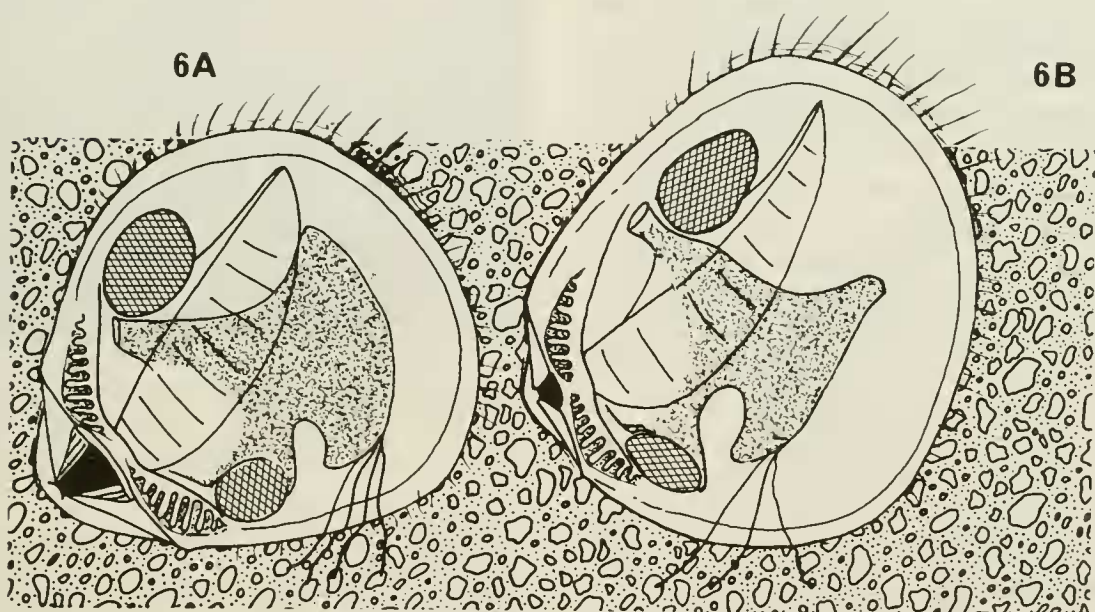
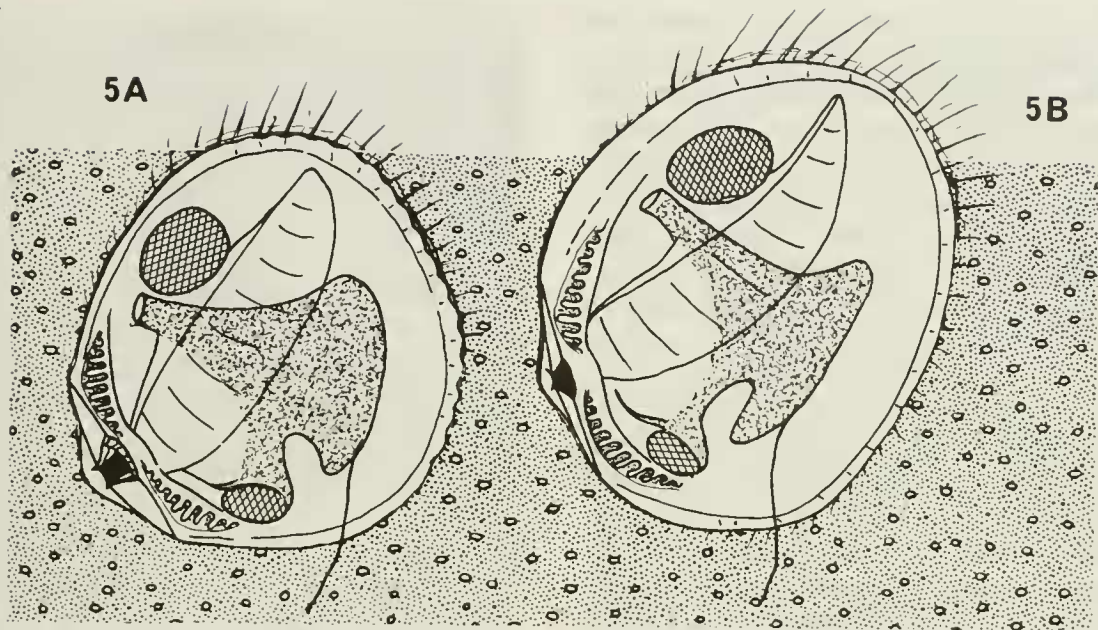
functional similarity: 1. **Limopsiform.** (M.C. I–M.C. VII). Shell thin, strongly oblique, hinge weak, heteromyarian condition advanced. Foot with a long toe, byssus functional, gill axis muscular. 2. **Glycymeriform.** (M.C. IX–M.C. X). Shell thick, oblique, hinge strong, heteromyarian condition moderate. Foot blade-like, byssus functional, gill axis weakly muscular. 3. **Abyssate.** (M.C. XI–M.C. XIII). Subequilateral, almost elliptical, hinge moderate, almost isomyarian. Foot blade-like, byssus not functional in adult, gill axis feebly muscular.

#### *Limopsiform group*

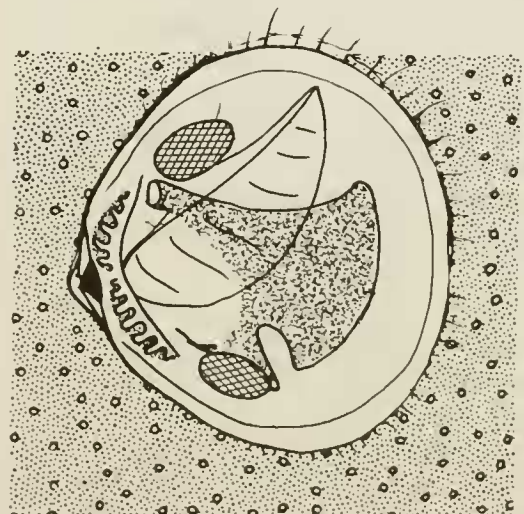
Within the limopsiform classes there is a series of linked progressive character changes which indicate a range of life modes from 'ploughing' through endobysate to epibyssate. This progression is linked to the strength and use of the byssus, involving related changes in pedal morphology and shell characters.

The ligaments found within the limopsiform group are of Types A, B and C (App. Fig. 1).





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FIGS. 5-8. Reconstructions of life positions. Fig. 5. Glycymeriform. A. *Limopsis multistriata* (M.C. IX). B. *L. bassi* (M.C. IX). Fig. 6. Glycymeriform. A. *L. loringi* (M.C. X). B. *L. eucosmus* (M.C. IX). Fig. 7. Abyssate Burrowing *L. lilliei* (M.C. XIII). Fig. 8. Abyssate Burrowing *L. vixornata* (M.C. XI).

However, there is apparently no relation between the ligament type and habits. In ligament Types A and B there are both ploughing and epibyssate species and a similar range occurs in species with the Type C ligament. The detailed function of these ligaments requires evaluation, but for the present, without suitable material, little can be done.

Ploughing (M.C. I-M.C. IV): The behaviour of *Limopsis aurita* (M.C. IV) in soft sediments is typical of the ploughing mode (App. Fig. 12). Effectively, the behaviour is crawling, with depth of penetration depending on the resistance of the substrate. The long toe is capable of considerable extension and the animal is progressively pulled across or into the substrate, there being no stationary burrowing motions. The long sole created by the extension of the foot into the toe and heel gives a stable crawling base. Conversely, this foot form is not adapted for efficient burrowing. The heteromyarian condition, weak hinge and weak ligament, are also indicative of a non-burrowing habit. The compressed shell acts as

a blade and aids substrate penetration, but if this is not achieved the animal is unstable in an upright position. The byssus, although weak, is frequently employed in *L. aurita* and gives some anchoring effect. The byssus activity is reflected in the presence of a small byssus

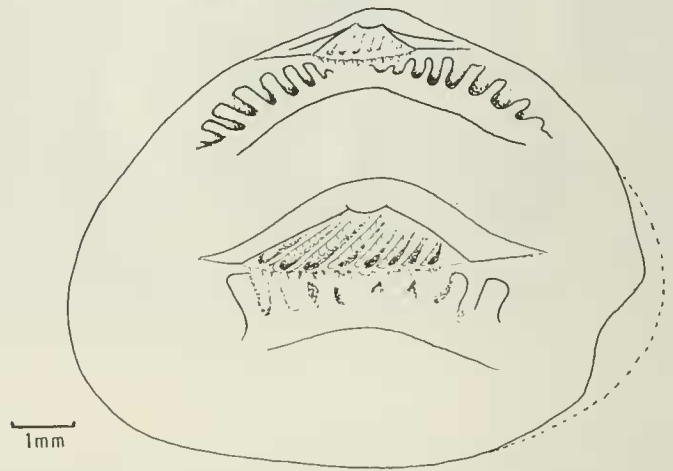


FIG. 9. *Limopsis minima* Sow. (= *oolithica* Buvignier) with ligament area enlarged to show remains of obliquely grooved ligament.

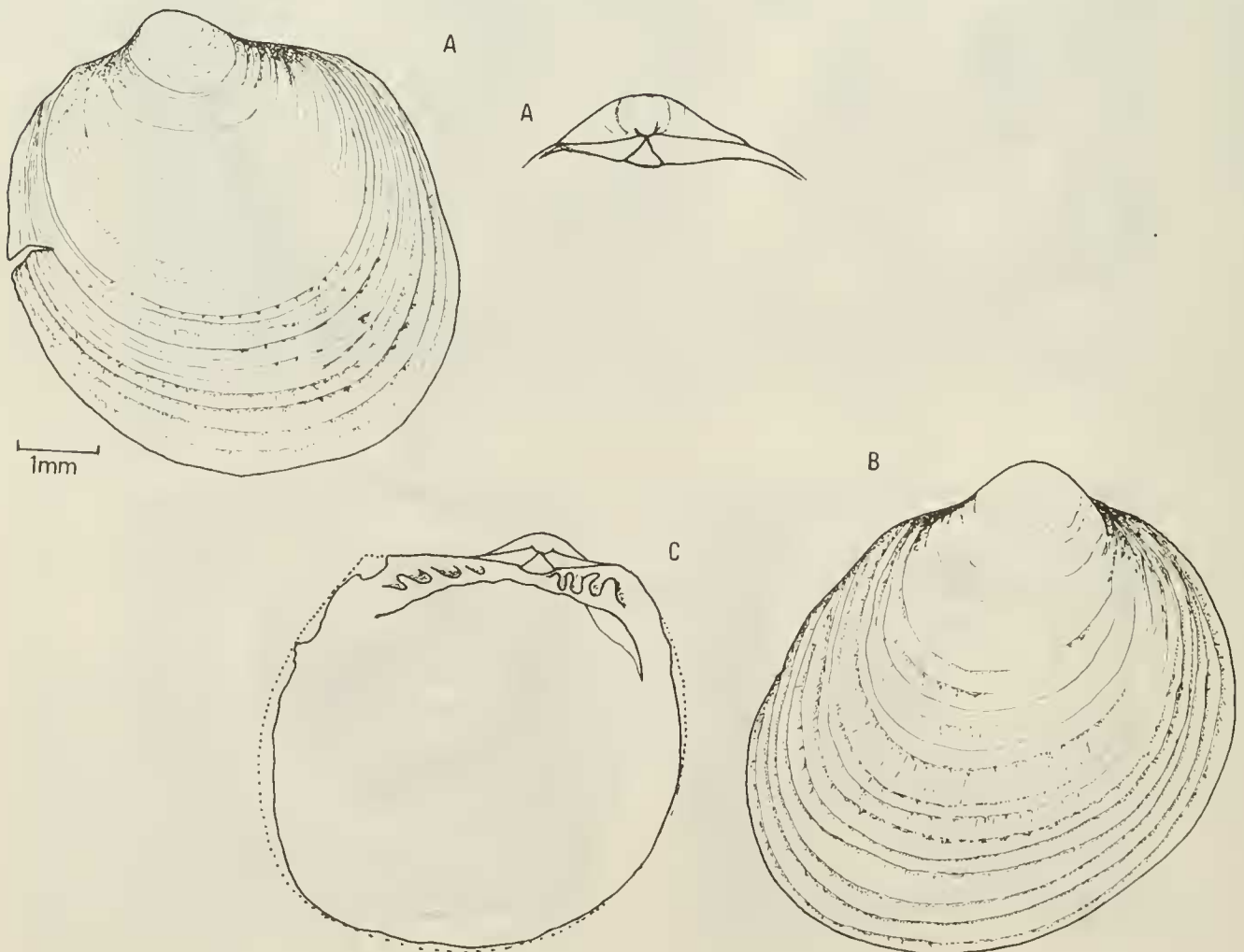
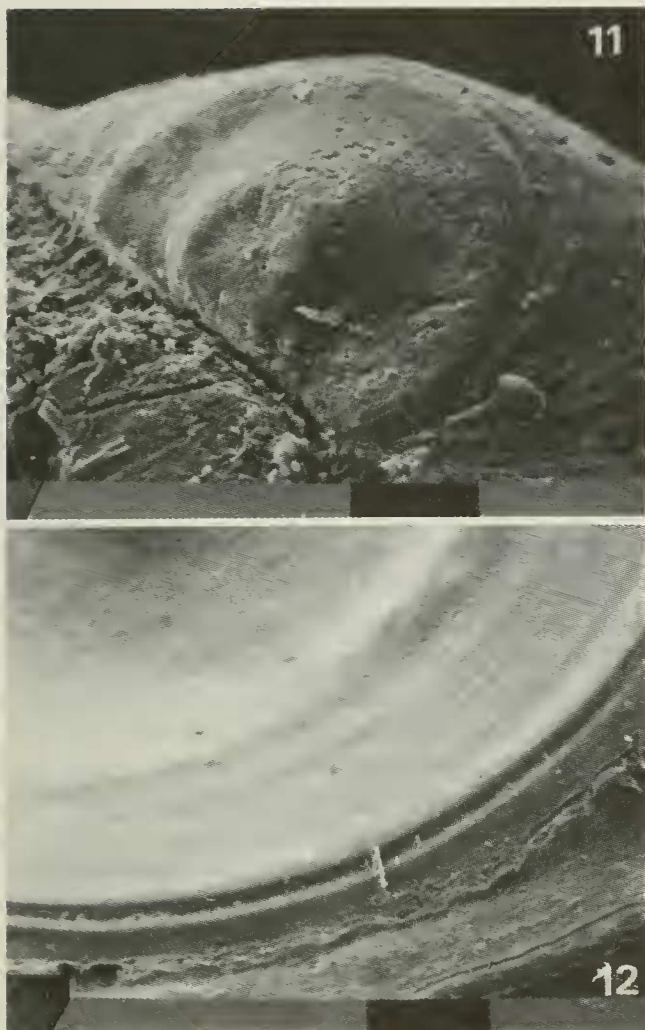


FIG. 10. Some early Cretaceous limopsids. A. *Limopsis albiensis* Woods. B. *L. coemansi* Briart & Cornet. C. *L. hoeninghausii* Müller.





FIGS. 11–12. *Nipponolimopsis decussata* (A. Adams). Capped prodissoconch (Fig. 11) and marginal locking groove (Fig. 12).

retractor element in the posterior pedal retractor (App. Fig. 11). A consequence of this variability in substrate penetration is the inconsistent positioning and size of the inhalant aperture. Oliver & Allen (1980b) observed that frequently the whole limit of the shell gape was open. This led to considerable amounts of unwanted matter entering the mantle cavity and this was frequently expelled by gill contraction and valve clapping. This behaviour explains the large amounts of axis muscle in *L. aurita* (App. Fig. 11). In soft sediments the gape was reduced and the mantle cavity was protected by interlocking edges of the periostracal interlocking edges of the periostracal bristles.

This apparently generalised form provides a good interpretive base. *Limopsis marionensis* (App. Fig. 2 and 5; M.C. I) is a considerably larger species, is more compressed and the anterior margin is more rounded. The two latter features further aid substrate penetration and stabilisation respectively. The posterior pedal retractor has no separate byssus element and

the rare occurrence of the byssus thread suggests that the ploughing habit is employed and is probably more efficient than in *L. aurita* (M.C. IV). Observations on another species (*L. tenella*) showed that the umbonal and posterior portions were most heavily infested, again adding to the premise that M.C. I species are semi-infaunal (Oliver & Allen, 1980b). M.C. I species are almost exclusively found in soft sediments where endobysate anchoring is least necessary. *L. marionensis* has been recorded from coarser substrates and here this species must be surface-living. In all substrates it is expected that frequent dislodgment will occur and that surface positions will not be uncommon.

In all characteristics other than the inner serrated margin and ligament, the species of M.C. II (App. Fig. 3) are identical morphologically to M.C. I and are also presumed to be ploughers. The serrated margin is a weak form of marginal crenulation which more commonly occurs in the endobysate and epibysate species.

The presence of the cleft in *Limopsis vaginata* and *L. cumingi* A. Adams (1862) (App. Fig. 4; M.C. III) is no doubt of some functional significance, but without direct observations it remains obscure. The ontogenetic development of the cleft (App. Fig. 7) clearly shows that it is analogous to the small indentations seen at either end of the dorsal area in many typical species. It is, therefore, tempting to associate the cleft with the hinge mechanics. In *L. vaginata* the hinge plate, because of its restriction to a shorter area, is more arched and probably stronger. The advantage of this in an otherwise ploughing form is obscure. Another consequence of the cleft is the spouting or projecting of the postero-ventral margin. Fig. 1 shows *L. vaginata* and a typical M.C. I form orientated along the same axis. In *L. vaginata* the major inhalant area is raised higher in the water column. This spouting effect may help to cut down the amount of substrate derived matter entering the mantle cavity.

Endobysate forms (M.C. V–M.C. VI): A more sedentary infaunal habit is evidenced in some of the smaller limopsiform species by the presence of a multiple, long, fine-stranded byssus and a separate byssus element (App. Fig. 13) in the posterior pedal retractor. The byssus threads have no terminal disc and have small sediment particles attached along their length. This strong evidence of endobysate attachment is substantiated by other features. The periostracal bristles are gener-

ally spicate (App. Fig. 9) and act in a manner similar to shell spines, i.e. as a stabilising mechanism. This type of periostracum no longer acts as a protective grid and the mantle margins in some species are more muscular, indicating their ability to form discrete inhalant and exhalant apertures.

The outline and relative tumidity are somewhat variable and this gives a variety of orientations to the endobysate species (Fig. 2). The majority are relatively compressed and have a tendency towards a straight anterior margin, e.g. *Limopsis cristata* and *L. affinis*. In *L. affinis* this development reaches its extreme, giving a pseudo-modioliform appearance. The orientation of this form is probably sub-surface with the greater part of the shell not buried. Shell epifauna data from Oliver & Allen (1980b) support this conjecture.

In the more rounded forms which in some, e.g. *L. oblonga* A. Adams, 1860 (App. Fig. 14), are relatively tumid, a deeper position is hypothesized. The rounded, less oblique outline is consistent with the burrowing species and the true ploughing forms. In muds, which are the most common habitat for these species, penetration would not be difficult. In fact, the tumidity may be a stabilising influence preventing the animal from becoming buried beyond the postero-ventral margin. *L. galathea* Knudsen, 1970 (M.C. VI) represents the extreme of this fixed infaunal habit (Oliver & Allen 1980b), the reduced heteromyarian condition, stubbly periostracum and relative tumidity are indicators of this. *L. galathea* lives in soft abyssal oozes where overpenetration is very likely.

The larger compressed species *Limopsis diegensis* Dall, 1908 (App. Fig. 10) with its thatched periostracum outwardly resembles a ploughing form; anatomically it is endobysate. This intermediate character probably reflects a more active habit as a plougher. Ploughing activity by the endobysate forms is probably common as all species possess a long-soled foot. Physical and biological disturbance is probably a frequent occurrence and the ability to crawl away and re-establish itself would be advantageous.

In all the endobysate forms the inner margin is evenly crenulated by raised ridges or nodules. In these small species this character is regarded as a counteracting mechanism to the weak hinge and ligament. It is presumed to prevent shearing of the valves which may be caused by physical or biological disturbance.

Epibysate forms (M.C. VII–M.C. VIII; Fig. 3): The epibysate mode is evidenced in the limopsiform group through the strength of the byssus and the classically associated shell characteristics of tumidity and anterior reduction (Stanley, 1972) (Fig. 4). The byssus consists of three to six short strap-like strands attached to a basal sheath. They have divided ends with no terminal discs, but have been observed firmly attached to particles of gravel. In M.C. VIII (App. Fig. 16), the outline of the shell is quadrate with a marked antero-dorsal straight margin. This straight edge gives a stable area on which the shell can rest. The tumidity of these forms is relatively great and this prevents toppling. The quadrate outline of M.C. VII (App. Fig. 15; *Limopsis minuta*) is less and it is presumed that this group is not so highly adapted to the epibysate mode.

In both M.C. VII and M.C. VIII the anterior reduction is advanced, but the anterior adductor and anterior hinge teeth are never lost.

The byssus retractor systems in the two classes are different. The minute forms of M.C. VIII have no separate byssus retractor element. No specimens have been available to carry out detailed anatomical studies; it is presumed that the posterior pedal retractor is large enough to assume this role. The condition may be even more extreme where the posterior retractor has its main muscle attachments to the byssus gland rather than to the base of the foot. In the larger M.C. VII class a highly specialized byssus retractor is present (App. Fig. 17) and this may be a function of the larger size, but may also be related to the less adapted shell outline. The less quadrate form of *Limopsis minuta* is less stable and to counteract this, the byssus retractor is stronger.

Marginal crenulations reach the peak of development in the epibysate forms and their restriction to the postero-ventral margin is undoubtedly linked to the high degree of anterior reduction. In these forms the hinge no longer acts as a major valve-locking mechanism, this being taken over by the posterior adductor. To prevent shearing around the adductor, a new pseudo-hinge is formed across the adductor utilising the now small true hinge at one end and the postero-ventral crenulations at the other.

Intermediate forms may be represented by *Limopsis elachista* Sturany (1899) which, while possessing a 'strap' byssus, does not become quadrate until late in its development. This species may be partially endobysate.



Unfortunately, no observations on live animals are available for this group and although Fig. 3C shows the minute quadrate form in a true epifaunal habit, this may not be correct. The comparable byssus strength of similarly-sized epibyssate arcaceans is much greater, e.g. *Bathyarca pectunculoides* (Oliver & Allen, 1980a), and consists of a single thick stalk. The epibyssate limopsids may, therefore, require some degree of support and could live in crevices or nestle at the base of larger sedentary epifauna. *Limopsis minuta* although normally taken from shell and coral gravels, has also been recorded from muds. These mud-dwelling species must be partially infaunal and Oliver & Allen (1980b) noted that some specimens did not develop the anterior straight margin and remained in outline very similar to *L. aurita*.

#### *Glycymeriform group*

The morphological features of classes M.C. IX (App. Figs. 18 and 20) and M.C. X (App. Fig. 21) are strongly convergent with those of the Glycymerididae. From the morphological features alone one could deduce the poor shallow burrowing ability of these forms and this is confirmed by the observations of Taylor (personal communication) and Tevesz (1977) (Figs. 5 and 6).

The anatomy of the foot is quite different from those of the Limopsiform classes and has only a very small toe and heel, being altogether blade-like and very muscular. The burrowing ability of this foot is aided by the large posterior retractor. The dominance of the posterior retractor is probably the cause of the reduced condition of the anterior retractor which has no or very little shell attachment. This is identical in *Glycymeris*. Since valve movements are important in burrowing, the adductor and hinge are both stronger. The former is evidenced in the reduced heteromyarian condition and the latter in the stronger hinge teeth which are set on a high arch. In general, both classes tend towards an equilateral outline; this too is a feature of the glycymeridids. In both classes the shell is thick, and this is necessary in arcoids not only to develop strong hinge and muscle attachments, but it is also needed to protect the animal when dislodged. Furthermore the thick shell gives protection from crushing predators (Vermeij, 1978).

Dislodgement is probably very common in this group, as noted by Taylor (personal com-

munication) and may be one of the stronger adaptive forces as it is for glycymeridids (Thomas, 1975). Unlike glycymeridids, the byssus remains functional, especially in M.C. X. This suggests that this class is subject to dislodgment and their occurrence on shell hash supports the theory that the habitat is subject to strong currents and consequent disturbance. M.C. IX species possess a very weak byssus by comparison, but they apparently prefer sandy or muddy sand substrates which are probably more stable. The prominent ribbing on the M.C. IX species such as *Limopsis multistriata* (Forskål, 1775) and *L. forteradiata* (Cotton, 1931) may act to stabilize the shell in these finer sediments.

The fixed sedentary burrowing mode confines the inhalant and exhalant apertures to a small area along the postero-ventral edge. The strongly muscular mantle margin in this region is capable of forming discrete apertures and regulating the currents. The intake of unwanted matter is, therefore, reduced and the cleansing actions are required to a lesser extent. This is reflected in the small amount of gill axis muscle in these forms (App. Fig. 6B). The periostracum, due to abrasion, is normally largely removed, but, if persistent, is only so around the postero-ventral margin where it still protects the current apertures.

*Limopsis bassi* Smith, 1885 (App. Fig. 19) and *L. eucosmus* Verco, 1907 (App. Fig. 22) represent intermediate forms between the limopsiform and glycymeriform groups, *L. bassi* being a M.C. IX associate and *L. eucosmus* to M.C. X. Both tend towards a more oblique form with a more advanced heteromyarian condition and the foot has a more strongly developed toe. The retractors, hinge and other shell characters remain glycymeriform. It is assumed that these intermediates are less capable burrowers and subsequently the extent of penetration is less. Tevesz (1977), however, reports that *L. soboles* (Iredale, 1931) behaves like *L. loringi* and from examination of figures only there is a similarity between the former species and *L. eucosmus*. In Figs 5B and 6B the intermediates are shown as only semi-infaunal, but may be able to completely burrow to the posterior shell margin.

#### *Abysate group*

The third group contains three classes which are apparently not closely related morphologically. They share an almost equi-

lateral outline, an almost isomyarian condition and an apparent lack of byssus function. These characters alone are sufficient to suggest a shallow burrowing mode. Classes M.C. XI (*Limopsis vixornata* Verco, 1907; App. Figs. 23 and 25) and M.C. XII (*L. brazieri* Angas, 1871; App. Fig. 26) share the slight prosogyrate condition. The hinge, dorsally attenuate shape, buttressed adductor and internally striate shell of *L. vixornata* cause it to resemble the *L. loringi* (M.C. X) class. Anatomically the foot and pedal retractors are similar also. The greater equilateral form and abyssate condition is, however, quite different, but it is not unreasonable to assume that *L. vixornata* represents an extension of the glycymeriform burrowing type to a more efficient free burrowing type (Fig. 8). *L. brazieri* with its elliptical outline probably represents one extreme development of the burrowing trend in the Limopsidae, but confirmation from anatomical data is required. No habitat details are available for either class but their sublittoral/shelf range and normal lack of periostracum suggests that they inhabit sands or coarser sediments.

*Limopsis lilliei* Smith (1885) (M.C. XIII; App. Figs. 24 and 27), although sharing the major characters of this group, differs in possessing a thin shell, covered by a pilose periostracum, in the relatively weak hinge and the complex ligament. The former differences can be related to the soft muddy sediments preferred by this class in which dislodgment and abrasion are likely to be less. The periostracum is invariably clogged by sediment and the fine erect hairs aid stabilization, through preventing either sinking or dislodgment. The weak hinge is unusual in burrowing limopsids, but the well-developed secondary ligament placed at the ends of the dorsal area are presumed to help in holding the valves together. The intact lamellar layer is much larger than in the ligament Types A-C. Combining the more efficient ligament and the large equal adductors suggests that this class is made up of relatively more efficient burrowers. It is expected that these forms would burrow up to their postero-ventral margins (Fig. 7). The mantle edge is especially thickened here and could form precise inhalant and exhalant openings. The gill axis musculature is almost negligible and shows a further progression of the condition seen in the glycymeriform group.

## EVOLUTION

The current extent of knowledge of the evolution of the Limopsidae is poor due to the limitations of the fossil record and lack of investigation. To examine all the available material is beyond the scope of this paper and reliance is placed mainly upon the published data. The collection of Mesozoic limopsids in the British Museum (Natural History) was examined.

Tevesz (1977) studied the problem of limopsid origins, proposing a neotenous derivation from the Grammatodontinae. Heinberg (1976, 1978) extensively examined an assemblage of late Cretaceous (Maastrichtian) limopsids; his study provides very significant data on form and radiation. The functional interpretations made by Heinberg (1979) do not entirely agree with those in this paper and consequently there are some revisions here. Heinberg (1979) underestimates the extent of endobyssate attachment and ploughing, postulating either epifaunal or infaunal habits. This study clearly shows that ploughing and endobyssate habits in soft substrates are the dominant limopsid life habits. Consequently, the homeomorphs of the Recent compressed, anteriorly reduced, heteromyarian forms are not always epibyssate as suggested by Heinberg but many are semi-infaunal endobyssate or ploughing species.

Cenozoic limopsids are more numerous but there are apparently no studies concerned with them alone.

### Origins

Tevesz (1977) placed the origin of the Limopsidae in the middle Jurassic (Bathonian) citing *Limopsis minima* (Sowerby, 1825) [= *oolithica* (Buvignier, 1852)] as the oldest known species. Tevesz places great emphasis on the ligament pit as a limopsid character and his interpretation rests strongly on its presence. *L. minima* and *L. oblonga* (Sowerby, 1825) are both well represented in the BMNH collection. Contrary to the specific name and small dimension of the type of *L. minima*, it reaches a maximum size of 20 mm. It is sub-quadrate with slight posterior extension, isomyarian and possesses a thick shell with an impressed ligament area. In the small species this ligament area resembles that of a limopsid, but in some of the larger,



better preserved specimens the area is marked by oblique grooves and ridges (Fig. 9). This ridged ligament area is consistent with the reduced duplivincular form seen in grammatodonts. Oblique grooves are not found in multivincular limopsid ligaments, any ridging found being vertical. The form of the juvenile ligaments in *L. minima* is typical of most juvenile arcaceans and in itself is not evolutionarily significant. There are no grounds, therefore, for assigning *L. minima* to the Limopsidae or for regarding this form as a more probable limopsid ancestor than any other grammatodont. A similar argument is applicable to *L. corallensis* (Buvignier, 1852) a late Jurassic species which has a distinct duplivincular ligament.

Arkell (1929–1936) describes an unnamed species from the late Jurassic (Oxfordian) strata near Pickering, Yorkshire, England. This species reaches 22 mm, is obliquely circular, but the hinge is not preserved.

It is not until the lower Cretaceous (Albian) that the first truly recognizable limopsid is found. *Limopsis albiensis* (Woods, 1899) is small—6 mm (Fig. 10A), obliquely circular, heteromyarian with a smooth sculpture and a small ligament pit. Overall it is an exact homeomorph of juvenile Recent ploughing species, e.g. *L. aurita*.

Although the exact origins of the Limopsidae have not been elucidated, it is important to note that whether *L. sp.* Pickering or *Limopsis albiensis* represents the ancestral form; both are obliquely circular. This indicates that the ancestral life habit was semi-infaunal and probably byssate.

### Radiation

The initial trend is seen in two species which occur in the Upper Albian, *Limopsis coemansi* Briart & Cornet, 1868 (Fig. 10B) and *L. hoeninghausii* (Müller, 1846) (Fig. 10C). *L. coemansi* is roundly oblique, oval and rather tumid whereas *L. hoeninghausii* is quadrate and tumid. These species show an initial radiation into the endobysate and epibysate modes.

Interpreting the shell character of Heinberg's (1979) species on the basis of the anatomical data in this paper it is possible to recognise the extent of the Late Cretaceous (Maastrichtian) radiation. The Limopsiform radiation is extensive: ploughing habits are

represented in *Limopsis misjæ* Heinberg, 1976, endobysate habits in *L. ravni* (Heinberg, 1976) and *L. augustae* (Heinberg, 1976). The respective Recent conchological homeomorphs of these would be *L. aurita*, *L. oblonga* and *L. cristata* and for both epibysate species *L. elachista*. It is of note that there are no large ploughing species in the white chalk assemblage. The quadrate epibysate species differ from Recent forms in lacking any marginal crenulation.

*Limopsis amandae* (Heinberg, 1976) is relatively tumid, but otherwise is typical of the ploughing form. This tumidity, as Heinberg notes, is indicative of an infaunal habit. However, given the strong heteromyarian condition of that species it seems doubtful whether the adductor strength would be sufficient to facilitate burrowing. A semi-infaunal habit is, therefore, proposed for *L. amandae*.

*Limopsis nanae* (Heinberg, 1976) is a minute species (2.6 mm) which possesses peculiar sub-concentric ridges on the inner shell margin. Heinberg postulates that the size negates any requirement for anterior reduction to facilitate epibysate attachment. However, *L. nanae* represents the juvenile form of numerous limopsids which are not necessarily epibysate. Probably all limopsiform species are able to crawl and the small size would aid this function (Tevesz, 1977) giving *L. nanae* a broad niche. Heinberg attaches no significance to the marginal concentric ridges but they appear to be analogous to the marginal ridge present in *Nippono-limopsis decussata* (Adams, 1862) (= *nipponica* Yokoyama, 1920) (Fig. 12). *N. decussata* has not been included in this paper because, due to the presence of a prodissoconch cap (Fig. 11), it is considered to be a philobryid. It was intended to make this observation the subject of a small paper, but it is now useful to mention it here. This form of margin is considered to be a valve locking mechanism and is apparently unique to the Limopsacea. The temptation to link *Limopsis nanae* to *N. decussata* is strong and would give added credence to Tevesz's (1977) theory that the Philobryidae arose neotenuously from the Limopsidae. The temporal and spatial separation of the two species is so large that such a link is doubtful, *N. decussata* being known only from the Pleistocene of Japan.

*Limopsis helenae* (Heinberg, 1976) has no

Recent homeomorphs and the epibyssate habit is accepted.

The Glycymeriform radiation is also apparent in the late Cretaceous (Newell, 1969) in the form with radial ribbing. Heinberg's glycymeriform species *Limopsis maggae* (Heinberg, 1978) is in contrast a smooth-shelled form. In the northern hemisphere the smooth-shelled forms are not apparent in the Cenozoic, whereas the ribbed variety is frequent, e.g. *L. scalaris* (Sowerby, 1825) (Eocene). In the southern hemisphere there are numerous smooth-shelled homeomorphs of *L. loringi* and *L. eucosmus* occurring from the Eocene onwards in the New Zealand and Magellanic provinces (Fleming, 1966). From the Cretaceous onwards there is an increase in maximum size of both groups of glycymeriform limopsids.

The limopsiform groups display little further radiation in the Cenozoic, the appearance of large ploughing forms in Recent times being the only event of significance. The epibyssate species and fixed endobyssate species remained small but did develop marginal crenulations.

The isomyarian groups have poor fossil records. M.C. XI (*Limopsis vixornata*) has a probable homeomorph in the Palaeocene of New Zealand, *L. microps* Finlay & Marwick, 1937 (Fleming, 1966). *L. brazieri* (M.C. XII) has a very short fossil record, *L. adamsiana* (Yokoyama, 1920) from the Pleistocene of Japan is probably a homeomorph. M.C. XIII (*L. lilliei*) has no fossil record and is presumably of relatively recent origin.

The fossil record of the limopsids is so scant that the formulation of phylogenies can only be hypothetical.

The origins of the family are not apparent but if for the sake of discussion one follows Stanley (1972), Tevesz (1977) and Morton (1978) and invokes a neotenous derivation of the Limopsacea, one must retain the Jurassic arcacean ancestry. This ancestor, whether a grammatodont or a cucullaeid, would presumably be isomyarian and retain the juvenile arcoid ligament in a small triangular resilifer. However, in the Limopsidae this ligament when large becomes multivincular and lacks chevrons. Furthermore the additions of new ligament material are in lateral positions unlike the central growth of the duplivincular ligament. Therefore one must not simply assign the limopsid's origin to a neotenic event but must also consider that the developmental characteristics of the ligament have changed.

This change must now be interpreted in view of Waller's (1978) classification of ligaments in which he considers all Limopsacean ligaments to be duplivincular. Waller (1978) does not indicate either ligament types B, C or D and clearly there is much more work to be done in this area before one can define the significance of limopsid ligaments. In addition, the initial radiation was towards the obliquely oval heteromyarian condition which is unlike all other arcoid tendencies as defined by Stanley (1972). Stanley's repetitive neotenic events consistently gave rise to trapezoidal epibyssate forms or orbicular sub-trapezoidal, shallow burrowing forms. The limopsid condition therefore represents a radical radiation away from the arcoid plan and is only paralleled in the Arcacea by a few members of the Striarcinae (*Ovalarca*) and Trinacriinae (*Stenzelia*). Although the neotenous derivation of the Limopsids is not discounted here it is felt that an oversimplification may be perpetuated and it is urged that the Jurassic arcoid radiation be reconsidered, especially with regard to the almost simultaneous appearance of the Arcidae, Noetiidae and Limopsidae.

The initial radiation of the Limopsiform groups into epibyssate, endobyssate and ploughing modes is well documented and has followed the classic patterns defined by Stanley (1972). The evolution of the ligament types A, B and C within the limopsiform groups is unclear. From the Recent forms there appears to be little difference in the radiation of those with Type A or C ligaments. This suggests that the selective value may be neutral and that these variations may have existed for a long time. The presence of the Type C ligament does, however, consistently occur in those Recent species which also possess crenulated margins. Such margins are not observed in the early fossils and therefore if the characters are linked there may be a case for the Type C ligament being secondary and forming a phyletic group. Conversely if the selective value of the Type C ligament is neutral it may well have arisen almost at random throughout the evolution of the limopsiform group.

The radiation into the glycymeriform and abyssate burrowing modes is apparently secondary. This is quite certain in the glycymeriform group where their appearance in the late Cretaceous and early Cenozoic is documented. The retention of a heteromyarian condition testifies to this but it must be noted that in



*Limopsis loringi* this condition is now slight. This reversal can be equated with the "Case II" evolution outlined by Stanley (1972) for the endobyssate to free-burrowing sequences seen in some of the Carditacea.

The radiation within the Glycymeriform species has resulted in two distinct groups: M.C. IX and M.C. X. Despite their similar habits and morphologies there is no fossil evidence to assume that they are part of a single lineage. These groups could well represent convergence within the Limopsidae. If so, this would indicate that such radiation occurred at least once in the now antipodean region and also in the now Mediterranean, Caribbean Indo-Pacific region. This has resulted in the distinct Recent distribution patterns of the two classes.

The complete isomyarian conditions noted in classes M.C. XI–M.C. XIII also appear to be secondary. There appears to be reason to accept this for M.C. XI and M.C. XII as a continuance of the glycymeriform radiation pattern. The fossil record is so scant that lineages are not considered. M.C. XIII (*Limopsis lilliei*), however, represents the appearance of ligament type D, associated with rather non-glycymeriform shell characters. In this class there are no fossil homeomorphs known and a gradual evolution of the Stanley Case II form seems untenable. This radiation may well be attributable to yet another neotenous event of the Case I type but associated with ligament changes.

In conclusion, the limopsids rapidly reached a peak in radiation by the early Cenozoic. This was achieved from a semi-infaunal stock radiating into the byssate modes to give rise to the Limopsiform classes with reversals into burrowing modes. These reversals may well have been numerous and thus one sees no evidence of a single lineage in the glycymeriform and abyssate burrowing groups. Coinciding with the early Cenozoic peak there appears to be a high diversity of species with a widespread shallow water distribution. This situation declined gradually so that one now sees the restrictive distributions and low species diversity of recent Limopsidae.

#### LIMITING FACTORS IN THE MORPHOLOGICAL RADIATION, DIVERSITY AND DISTRIBUTION OF LIMOPSIDS

Despite the functional radiation into ploughing, endobyssate, epibyssate, glycymeriform and burrowing habits, the morphology of the

limopsids has remained remarkably conservative. The functional diversity has been achieved through relatively small changes in shell form and anatomy. The relatively high functional diversity has, however, not been paralleled by a high Recent species diversity, there being at the most sixty valid species. Of these, at least seventy percent are semi-infaunal, either ploughing or endobyssate. Only eleven percent are epibyssate, twelve percent glycymeriform and eleven percent non-glycymeriform burrowers. In comparison with other Limopsacea there are at least eight times as many glycymeridids as glycymeriform limopsids.

Distributionally, the limopsids are limited—in the case of the limopsiform group, bathymetrically and the burrowing groups, geographically.

In the Atlantic Ocean the limopsiform species are found almost exclusively from the continental margin zone to the abyss, and never occur in shallow shelf waters. Exceptions to this are few; some polar emergence occurs in Norwegian fjords and the epibyssate quadrate *Limopsis antillensis* occurs in relatively shallow waters in the Caribbean. The Japanese zonation (Okutani, 1968) is similar, although the outer shelf is inhabited by some species. Only in the Antarctic do limopsiform species occur widely on the shelf (Dell, 1964). In general, the Limopsiform species are restricted to cold water and normally do not occur on the shelf.

The ribbed glycymeriform class is not deep water and occurs from the littoral to 400 m. This class is, however, geographically restricted to the Indo-Pacific and Mediterranean (Coen, 1931). The smooth-shelled glycymeriform class is restricted to the shelf and continental margin zone and is endemic to southeast Australia. The non-glycymeriform burrowing classes are similarly restricted geographically, two classes being endemic to southeast Australia and the third to Antarctica.

The Limopsidae with their restricted morphological diversity and distributional limitations could be considered a relatively unsuccessful family especially in their degree of attainment of the epibyssate and burrowing habits. The semi-infaunal forms are more numerous but in a life mode which has been abandoned by the majority of the Recent bivalves. The mechanism and extent of these limitations warrant further analysis for each major functional group.

The glycymeriform limopsids represent the initial radiation into the burrowing habit. This occurred very soon after the appearance of the Glycymerididae (Aptian/Albian). However, despite this almost equal time scale, there is a marked contrast in the relative success of the two groups.

Thomas (1976) showed the glycymeridid duplivincular ligament to be too weak to enable efficient burrowing and with the result that the animals were subject to repeated dislodgment. They are therefore not only adapted to survive the subsequent physical and predation pressures, but also to rapidly re-establish themselves in the substrate. The shells are consequently large, thick and orbicular with a strong hinge. As there is considerable convergence between the two groups, one can expect similar limitations to operate. The weakness of the glycymeridid ligament involves a combination of an inherent structural frailty with allometric growth. The strength of the limopsid alivincular ligament could not be measured as no live specimens were available. The glycymeriform limopsid ligament (Type A) is always formed in a very shallow resilifer and one never observes the deep resilia seen in *Ostrea* or *Vulsella*. This shallow ligament area is reminiscent of the typical arcoid structures and may well not possess the qualities of non-arcoid types. It is assumed here that the limopsid ligament is no more efficient than the duplivincular, especially with regard to their similarities in length of attachment, thickness of non-split layers and degree of umbonal growth. Allometric relationships between the ligament and shell of limopsids can be shown. In two ploughing species, *Limopsis aurita* and *L. marionensis*, results for mean log-log reduced major axis regressions indicated allometric relationships of ligament height, length and area with shell height. Results for *L. aurita* ligament areas were a correlation coefficient of 0.94 and a slope of 3.09 where a slope of 2 would be considered isometric for a linear-area relationship. Results for ligament heights and lengths separately were for *L. aurita*: ligament height  $r = 0.93$ , slope 1.54; ligament length  $r = 0.94$ , slope 1.58 and for *L. marionensis*: ligament height  $r = 0.95$ , slope = 1.35; ligament length  $r = 0.96$ , slope = 1.57. In these results the parameters are both linear and have an expected slope of 1.0 for an isometric relationship. The consequences of allometric growth are rapid dorsal splitting of the ligament (Trueman, 1969) and the re-

sulting ventral growth which interferes with the hinge. In glycymeridids the replacement is central but in large limopsids where the ligament becomes multivincular, replacement is also in lateral sites. Consequently, ventral encroachment is more widespread in the limopsids, so much so that in some large specimens (60 mm) of *L. marionensis*, no well-formed hinge teeth remain. Glycymeridids, however, may attain a much greater size (120 mm) without such severe tooth loss. It is noted that in glycymeriform limopsids multivincular structures are never developed and this may reflect the need to maintain a strong hinge. Furthermore, the multivincular ligament involves considerable elongation of the dorsal area with consequent changes in shell outline. This has been classically shown in *Perna* (Trueman, 1954) but is also true to a lesser extent here as evidenced in the ontogenetic changes seen in *L. tenella* (Oliver & Allen, 1980b) and *L. marionensis*. Such changes in outline would severely impair the burrowing ability of glycymeriform limopsids.

In these limopsids most growth is ventral and thus one observes deeply cleft dorsal areas and dorsally attenuated forms. This developmental restriction may therefore account for the small size of glycymeriform limopsids. This in itself may be disadvantageous as the smaller shells may be more prone to attack by crushing predators, a situation which (Vermeij, 1978) may contribute to the limited success of the limopsids in shallow water.

An additional disadvantage inherent in the glycymeriform limopsids is their derivation from a heteromyarian stock. Although this condition is reduced in recent forms there must be restrictions to burrowing caused by the weakness of the anterior adductor and the unequal forces created by this condition. The glycymeridids arose as an isomyarian group and have thus not been influenced in this manner.

The few isomyarian burrowing limopsids that exist are small forms. *Limopsis brazieri* and *L. vixornata* have a structural affinity with the glycymeriform group and are therefore believed to be subject to the same adaptive restrictions. Despite the isomyarian condition of these groups, their diversity and distribution is more limited than that of the glycymeriform group. This adds more credence to the hypothesis that the ligament structure is the major adaptive restriction. The Antarctic isomyarian group is, in contrast, widespread in its endemic province and also occurs in large



numbers to the extent that they may be the dominant bivalve in many samples. These species, e.g. *L. lilliei*, contrast morphologically in possessing a weak, thin shell with a weak hinge. Considerable ventral encroachment occurs in these forms and an edentulous space is rapidly developed, restricting the number of teeth to 3–5 on either side. The alivincular ligament is proportionately large and may be aided by the secondary ligament areas on the dorsal areas. These secondary areas may also strengthen the hinge as they lie immediately above the remaining hinge teeth. It has already been argued that such a thin-shelled, weak-hinged form is not viable and that the limopsid ligament is incapable of providing the mechanism for efficient burrowing. But here is an apparently successful burrowing limopsid. Mechanics alone cannot explain this anomaly. An examination of the Antarctic fauna highlights some contrasting competitive pressures experienced by non-siphonate, shallow burrowers. The Antarctic bivalve fauna has a unique make-up and has few siphonate suspension feeders (Powell, 1960; Dell, 1964). Furthermore, the diversity of non-siphonate burrowers is not as high as in temperate or tropical regions. It is probable, therefore, that the inefficient burrowing limopsids are subject to less competitive pressure in the Antarctic province. The Antarctic is unusual in that the fauna as a whole is impoverished and in particular lacks any benthic decapod Crustacea (Vermeij, 1978). Following Vermeij (1978) it can be argued that the lack of crushing predators has not necessitated the evolution of heavy, strong-hinged shells. Consequently ligament encroachment on the hinge in *L. lilliei* would not be too disadvantageous in relation to predation. Allometric ligament growth could then proceed, creating a stronger ligament for more efficient burrowing.

In comparison with other bivalve groups, the limopsiform classes are poorly adapted. The endobysate class has not paralleled the Modiolidae, Pinnacea or Pteriacea and a similar condition occurs between the epibysate class and the Mytilidae and Arcidae. The semi-infaunal classes do have analogues in the Palaeozoic, represented by some members of the Cyrtodontidae, Inoceramidae, Modiomorphacea and Carditacea, but few in the Recent. Stanley (1972) discusses the Palaeozoic and Mesozoic decline of the semi-infaunal bivalve and its replacement by highly adapted infaunal burrowing forms. A

consequence of this decline was the emergence of the epibysate bivalves during the late Palaeozoic and Mesozoic.

In the Mesozoic there must have been considerable adaptive pressure to radiate into the two highly adapted life modes of burrowing and epibysate attachment. The Limopsidae, arising as semi-infaunal species, rapidly responded to this pressure, reaching their peak as represented by the monomyarian *Limopsis augustae* in the late Cretaceous. From this point the epibysate and endobysate limopsid radiation remained static and the highly adapted byssate forms were never paralleled. Apparently unable to adapt further, the limopsids were at a considerable disadvantage and could not compete with the now dominant advanced byssate forms. Consequently the limopsiform classes were restricted to zones of higher stability and less competition—thus their deep water bathymetric range and occurrence in the low diversity, highly endemic Antarctic fauna. This limitation is very close to that experienced by the Brachiopoda and, at least in the Atlantic and Antarctic, the co-occurrence of limopsids and brachiopods is high (personal observations).

The mechanism preventing further limopsid radiation into the epibysate and endobysate habits is probably a function of the degree of anterior reduction. The extent of anterior reduction in the Arcacea is limited by the functional and growth constraints of the duplivincular ligament (Thomas, 1978a, 1978b). As limopsids possess an alivincular ligament this mechanism may at first not appear to be relevant, a view which was supported by Heineberg (1979).

Anterior reduction in limopsids necessitates reduction of the hinge teeth and dorsal area. In mytiliform bivalves this is of little consequence as the ligament is strong enough to hold the valves together and to articulate them. The limopsid alivincular ligament is restricted to a very shallow triangular resilifer displaced on the dorsal area and is, therefore, not suited to maintain valve adhesion without hinge teeth. However, the Philobryidae, which accepting Tevesz (1977) and Morton (1978) are derived from Limopsidae, have succeeded in radiating into edentulous mytilid homeomorphs via a progression from the limopsid-like genus *Cratis* to *Cosa* to *Philobrya*. The significant feature of epibysate radiation in both the Limopsidae and Philobryidae is the universal small size of the shells. This suggests that the edentulous, anteriorly re-

duced form is attainable only through miniaturization and this leads one to consider again the growth characteristics of limopsids. Combining the effects of the anterior reduction on the size of the dorsal area and number of hinge teeth with the allometric ligament, it is observed that the two are mutually exclusive. As anterior reduction diminishes the size of the dorsal area, it reduces the potential size of the ligament. In very small species this effect is negligible. However, as the linear dimension of the shell increases, the limitation of the ligament size is rapidly increased, the counteracting forces soon preventing further growth.

The limitations of the limopsid radiation, their recent diversity and distribution therefore appear to be a function of inherent morphological constraints. These constraints are primarily the inefficient alivincular ligament and the lack of any siphonal development. Some minor evolutionary events such as the initial heteromyarian condition may have contributed to the limitation of the family. However, competitive and predation pressures have also played a modifying role. These in general have been restrictive, resulting in the absence of semi-infaunal species from shelf waters and the further restriction of burrowing species. In the case of the Antarctic, such pressures are reduced and one observes a more diverse and prominent limopsid element in the fauna.

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#### KEY TO ABBREVIATIONS USED IN APPENDIX ANATOMICAL FIGURES

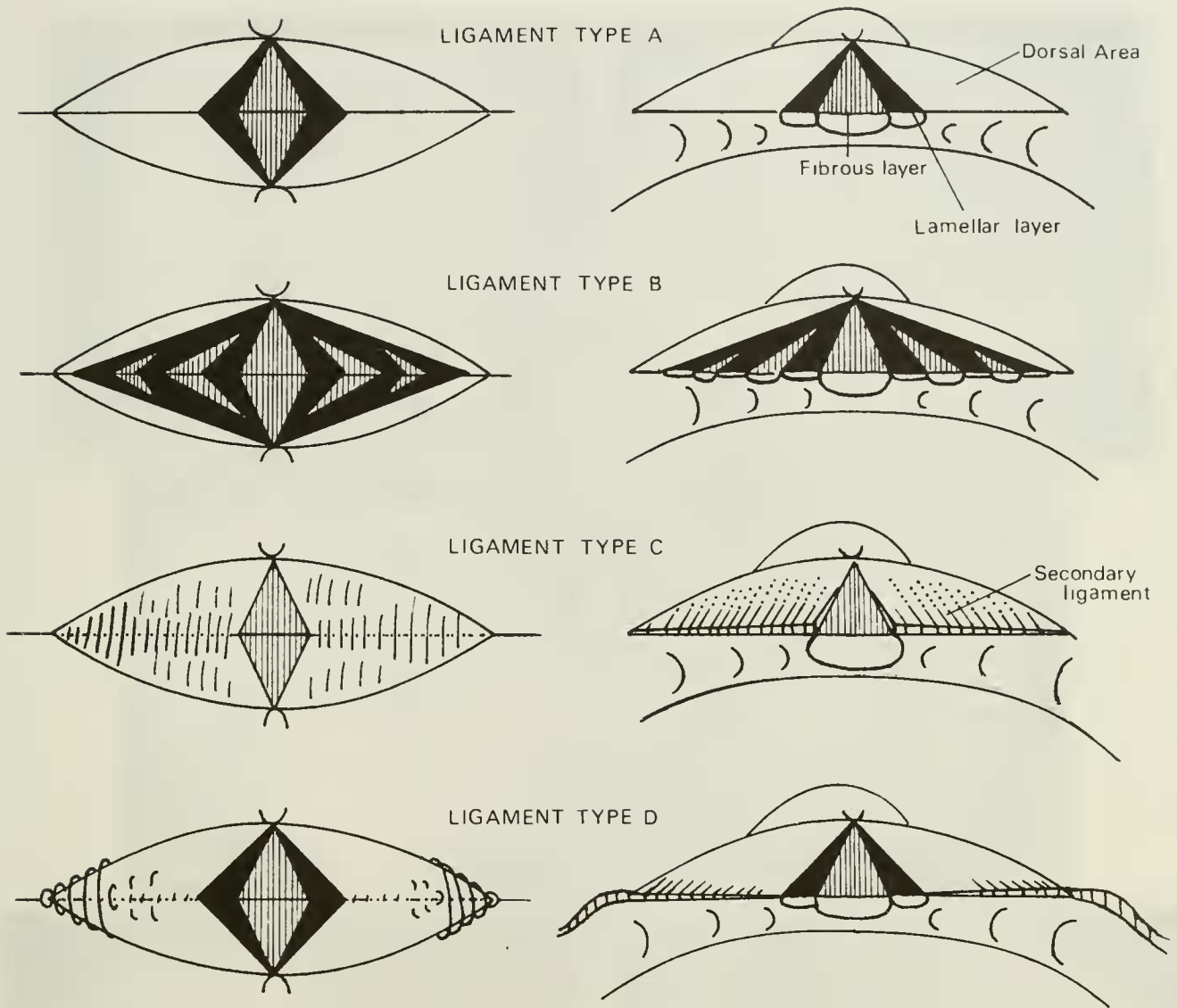
A	Anus
AA	Anterior adductor muscle
ARM	Anterior retractor muscle
B	Byssus
BRE	Byssus retractor element
BRM	Byssus retractor muscle
CT	Connective tissue
DG	Digestive gland
F	Foot
G	Gill
GD	Gonad
GA	Gill axis
GAM	Gill axis muscle
H	Heart
HG	Hind gut
K	Kidney
KD	Kidney duct
ME	Mantle edge
MN	Mantle nerve
P	Palps
PA	Posterior adductor muscle
PPM	Pedal protractor muscle
PRM	Posterior retractor muscle

#### APPENDIX: MORPHOLOGICAL CLASSES OF RECENT LIMOPSIDS

To present all the morphological data on fifty species would be confusing and consequently the species have been divided into classes of similar morphology. These classes cannot be rigidly defined and therefore there are some intermediate species. These are described separately only if they provide significant additional data. There are thirteen distinct classes which require definitions. The descriptions have been confined to concise diagnoses, using only characters of functional significance.

Some of the shell characters of the Limopsidae have not been adequately defined before. This has not only given rise to the con-





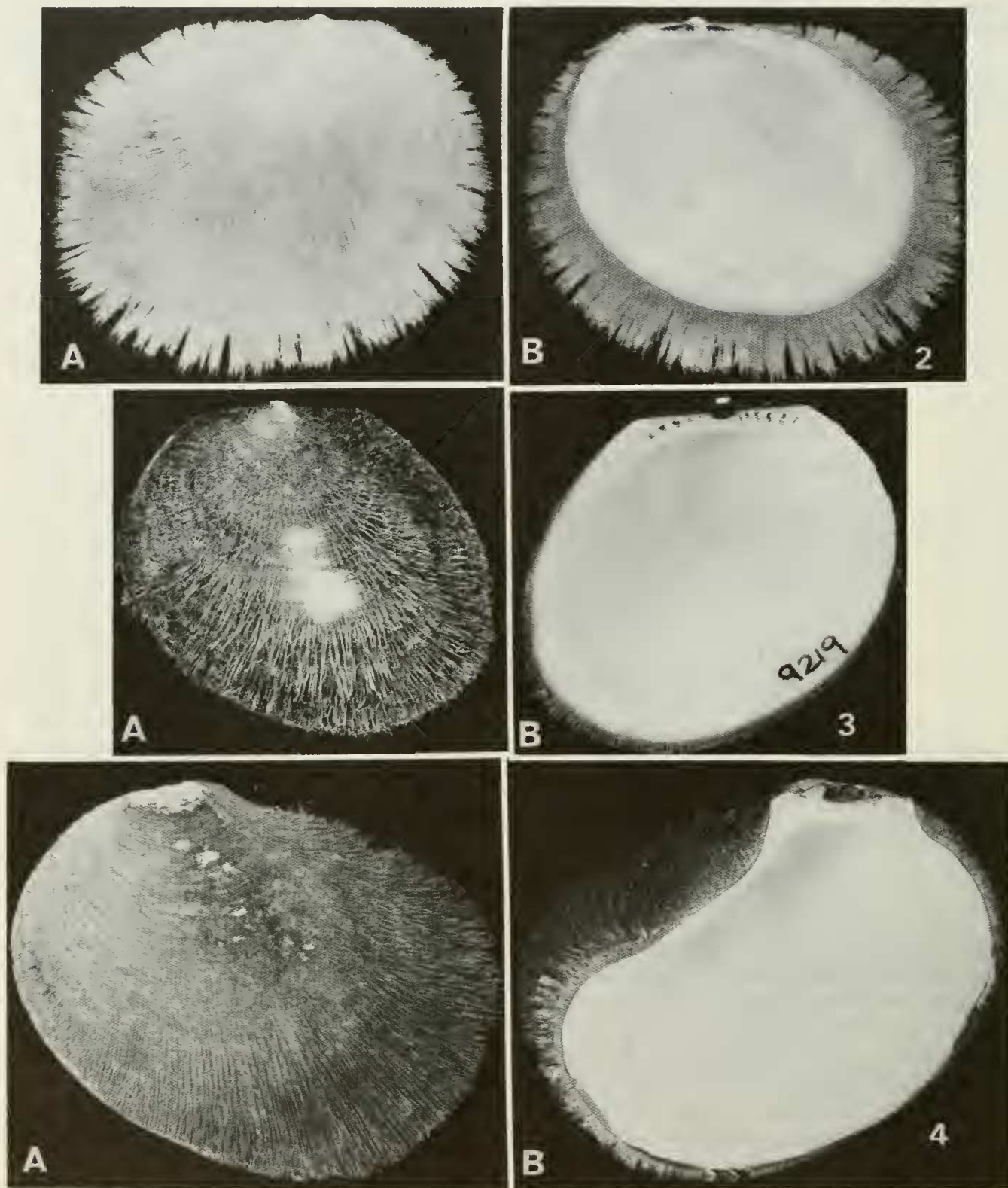
APP. FIG. 1. Ligament structures within the Limopsidae.

fused state of limopsid systematics, but has also obscured functional interpretation.

**Ligament:** The ligament in the limopsids, although typically alivincular (Trueman, 1969), is not always of the simple amphidetic type. There are four distinct forms (Oliver, in prep.) in which the disposition of the fibrous and lamellar layers differ; there is also a secondary ligament in some. The nature of the secondary ligament is uncertain and at this moment it is not known whether it is periostracal or a fusion layer. **Type A.**—Amphidetic alivincular: Primary ligament in a shallow resilifer, remainder of dorsal area covered by undifferentiated periostracum (App. Fig. 1). **Type B.**—Amphidetic multivincular: Primary ligament of multiple lamellar and fibrous segments all in shallow resilifer, remainder of dorsal area covered by undifferentiated periostracum (App. Fig. 1). **TYPE C.**—Primary ligament of fibrous layer only in a relatively deep and narrow resilifer. Dorsal area

covered by a thick layer of presumed secondary ligament joining the whole length of the dorsal area. The dorsal area may, however, be covered by the lamellar layer (App. Fig. 1). **Type D.**—Primary ligament of the amphidetic alivincular form (Type A). Dorsal area covered with a secondary ligament which is especially thickened at the ends of the hinge plate (App. Fig. 1).

**Marginal crenulations: Type A.**—Nodular, margin marked by alternating nodules and pits or ridges and troughs. Distinguishing ridges and nodules are impractical due to ontogenetic changes from one to the other. **Type B.**—Serrated, margin smooth except for fine serrations on its inner edge. This type is probably formed from Type A by overgrowth as the shell increases in size. **Type C.**—Fluted, the inner margin is more or less smooth except for weak undulations or corrugation which coincide with the radial ribs of the external sculpture.



APP. FIG. 2. *Limopsis marionensis* Smith. Baie de Penguins, Antarctica. IRSNB. Diam. 65 mm. APP. FIG. 3. *Limopsis chuni* Thiele & Jaeckel. Natal, South Africa. NM. Diam. 30 mm. APP. FIG. 4. *Limopsis vaginata* Dall. Bering Sea. IRSNB. Diam. 35 mm.

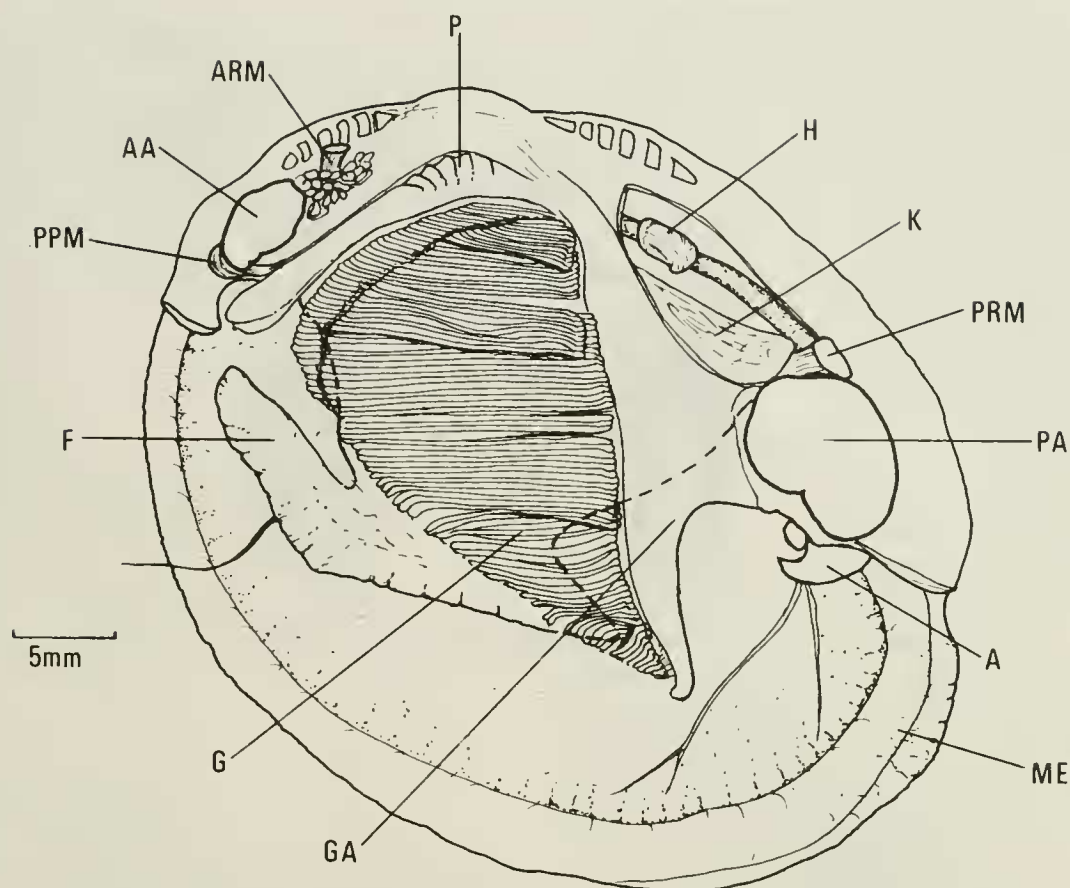
**Periostracal bristles: Thatched.**—Long fine bristles lying flat against the shell and forming a wide fringe. **Spicate.**—Short blade-like bristles standing more or less erect and not forming a wide fringe. **Lanceolate.**—Long needle-like bristles standing more or less erect and not forming a wide fringe. **Stubby.**—Short blunt coarse bristles standing

erect from shell. **Pilose.**—Moderately long very fine bristles, dense, standing erect.

#### Morphological Class I

Diagnosis: Larger species 20–60 mm max. diam. Equivalve, compressed, inequilateral, becoming obliquely oval or obliquely circular,





APP. FIG. 5. Gross anatomy of *Limopsis marionensis* Smith (left mantle removed).

i.e. strongly extended posteriorly. Shell thin. Sculpture weak, of concentric lines cut by radially arranged markings corresponding to periostracal bristle insertions. Periostracum thatched. Ligament (Type A) variable, becoming large or multivincular (Type B) in big specimens of large species. Dorsal area typically long, narrow and not deeply cleft, but may widen disproportionately. Hinge weak with numerous small teeth set in two series on a low arch, an edentulous space of variable size is present. Heteromyarian condition advanced, the anterior adductor is reduced and possesses a weak scar-umbonal ridge (myophore). Internal margin smooth (App. Fig. 2).

Foot with prominent toe and heel. Pedal retractors not large. Byssus gland active, producing a single long fine thread without any terminal disc. The byssus is rarely observed and is usual only in juveniles. Gill axis orientated obliquely to the hinge plate, highly muscular. Palps small with few weak sorting ridges. Mantle margin thickened postero-ventrally but not greatly (App. Figs. 5 and 6).

Habitat: Typically from sands, muds and oozes, but also from gravels.

Bathymetric range: 50–5500 m.

Distribution: cosmopolitan, but absent from the Arctic Ocean.

Species complement: *Limopsis marionensis* Smith, 1885; *L. tajimae* Sowerby, 1914; *L. dalli* Knudsen, 1970; *L. tenella* Jeffreys, 1876 (= *pelagica* Smith, 1885); *L. ruizana* Rehder, 1971; *L. surinamensis* Oliver & Allen, 1980b; *L. zonalis* Dall, 1908.

Tentatively included are *Limopsis janeiroensis* Smith, 1915; *L. indica* Smith, 1885; *L. siberutensis* Thiele & Jaeckel, 1931 and *L. paradoxa* (Iredale, 1931).

#### Morphological Class II

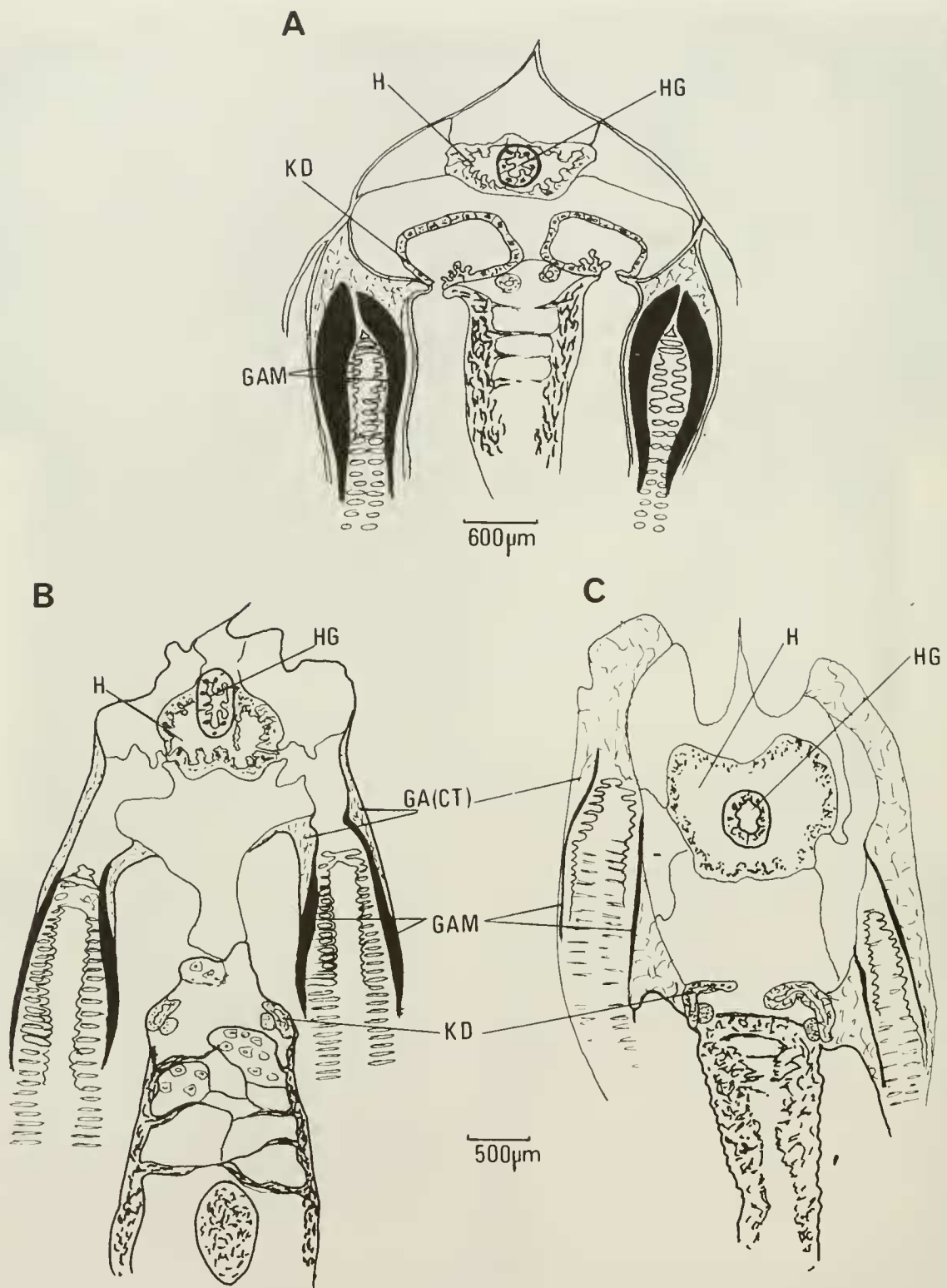
Diagnosis: Like M.C. I except that the sculpture is stronger and the periostracum a little coarser. Inner margin serrated. Ligament Type C. Anatomy essentially as in M.C. I (App. Fig. 3).

Habitat: Sands and muds.

Bathymetric range: 70–500 m.

Distribution: Indian Ocean (East and South Africa) and Korean Sea.

Species complement: *Limopsis chuni* Thiele & Jaeckel, 1931; *L. sansibarica* Thiele & Jaeckel, 1931; *L. belcheri* (Adams & Reeve, 1850).



APP. FIG. 6. Transverse sections through the region of the heart to show comparative extent of the gill axis musculature. (A) *Limopsis tenella* (Limopsiform). (B) *L. multistriata* (Glycymeriform). (C) *L. lillei* (Burrowing).

### Morphological Class III

Diagnosis: Like M.C. I except for the presence of a cleft formed by an indentation of the postero-dorsal shell margin. The cleft appears in juveniles as a small notch below the end of the dorsal area and increases in size with growth. There is a much smaller anterior cleft

in *Limopsis cumingi*. Ligament Type A. Anatomically similar to M.C. I (App. Figs. 4 and 7).

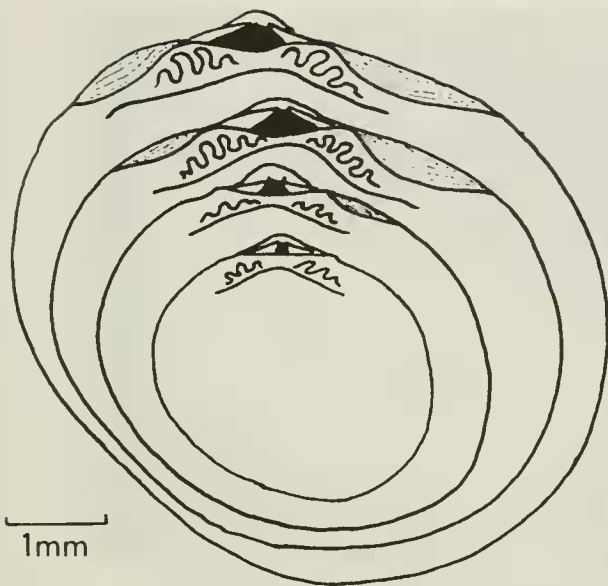
Habitat: Fine sands and muds.

Bathymetric range: 80–650 m.

Distribution: North Pacific (Alaska-Japan).

Species complement: *Limopsis vaginata* Dall, 1891; *L. cumingi* A. Adams, 1862.





APP. FIG. 7. Growth series of *Limopsis cumingi* A. Adams to show development of the clefts.

#### Morphological Class IV

Diagnosis: Medium-sized species: diam. 12–20 mm. Compressed, becoming strongly and obliquely oval. Periostracum thatched. Shell moderately thick. Ligament Type A. Hinge moderately strong, teeth larger than those in M.C. I. Heteromyarian condition advanced, greatly reduced anterior scar with well developed myophore. Anatomy as in M.C. I except that the posterior pedal retractor is slightly divided into byssus and pedal elements, the former being far the weaker. Byssus of a single long fine thread which is frequently observed (App. Figs. 8 and 11).

Habitat: Muddy gravels, shell gravels, sands and muds.

Bathymetric range: 100–1300 m.

Distribution: Atlantic Ocean and Japan.

Species complement: *Limopsis aurita* (Brocchi, 1814); *L. sulcata* Verrill & Bush, 1898; *L. obliqua* A. Adams, 1862.

Some of the smaller species included in M.C. I may belong here but the anatomical characters are not known, e.g. *Limopsis indica*, *L. janeiroensis*.

Habits: The following behaviours of *Limopsis aurita* were observed by Oliver & Allen (1980b):

In mud: *L. aurita* ploughs through the sediment surface penetrating only to a depth marked by a line through the umbos and postero-ventral margin. No burrowing movements were observed. When ploughing

ceased, most specimens remained in an upright position and produced the fine byssus (App. Fig. 12).

In sand: A similar behaviour occurs, but penetration is much less and the byssus is not able to prevent the animals from falling onto one valve (App. Fig. 12).

On gravel: The crawling persists, but no penetration is effected and the byssus is cemented to stones. In many cases the animals suspended themselves from larger stones hanging freely in the water (App. Fig. 12).

#### Morphological Class V

Diagnosis: Small species: diam. 5–12 mm. Compressed, inequilateral, becoming obliquely oval, occasionally obliquely circular, some developing a straight anterior margin. Shell thin, sculpture weakly decussate. Periostracal bristles stout, lanceolate or spicate, arranged in distinct radial or concentric patterns, persistent especially postero-ventrally. Ligament Type C. Hinge weak, teeth small on a low arch. Heteromyarian condition advanced, small anterior scar with weak myophore. Internal margin evenly crenulated, nodular. Anatomically similar to M.C. IV but the divided posterior pedal retractor has a stronger byssus element. The byssus consists of 3–6 long fine threads. Mantle margin thickened postero-ventrally (App. Figs. 9 and 13).

Habitat: Sands, muds and oozes.

Bathymetric range: 50–2500 m.

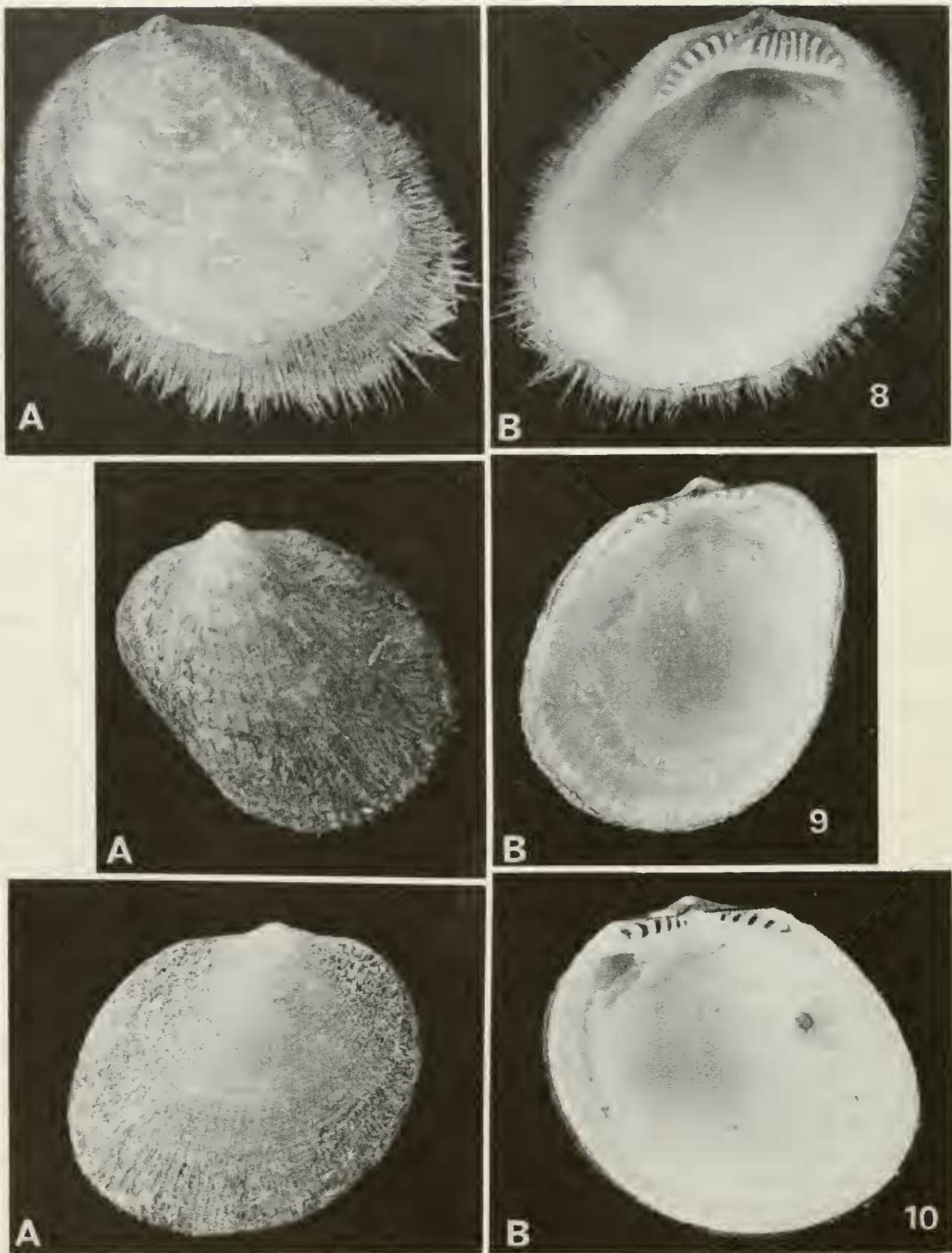
Distribution: Cosmopolitan except for the Arctic Ocean.

Species complement: *Limopsis affinis*, Verrill, 1885; *L. cristata* Jeffreys, 1876; *L. erecta* Hedley & Petterd, 1906; *L. idonea* (Iredale, 1931); *L. intermedia* Oliver & Allen, 1980b; *L. longipilosa* Pelseneer, 1903; *L. perieri* Fischer, 1870; *L. scabra* Thiele, 1912; *L. spicata* Oliver & Allen, 1980b; *L. lanceolata* Oliver & Allen, 1980b; *L. tasmani* (Dell, 1956).

The following species are tentatively included: *L. diazi* Dall, 1908; *L. mabillana* Dall, 1908 and *L. stimpsoni* Dall, 1908.

*Limopsis diegensis* Dall, 1908 (App. Figs. 10 and 13)

This species closely resembles M.C. V species both in shell and anatomy. It is larger, reaching 15 mm in diam. and possesses a 'thatched' periostracum. It is obliquely circular rather than obliquely oval.



APP. FIG. 8. *Limopsis aurita* Brocchi. Bay of Biscay. MNHNP. Diam. 15 mm. APP. FIG. 9. *Limopsis affinis* Verrill. Off New England, U.S.A. USNM. Diam. 10 mm. APP. FIG. 10. *Limopsis diegensis* Dall. Off California. USNM. Diam. 12.5 mm.

*Limopsis oblonga* A. Adams, 1860 (App. Fig. 14)

This is another species with an evenly crenulate margin and a somewhat spicate periostracum. It is, however, larger, reaching 15 mm in diam. and is relatively a little tumid.

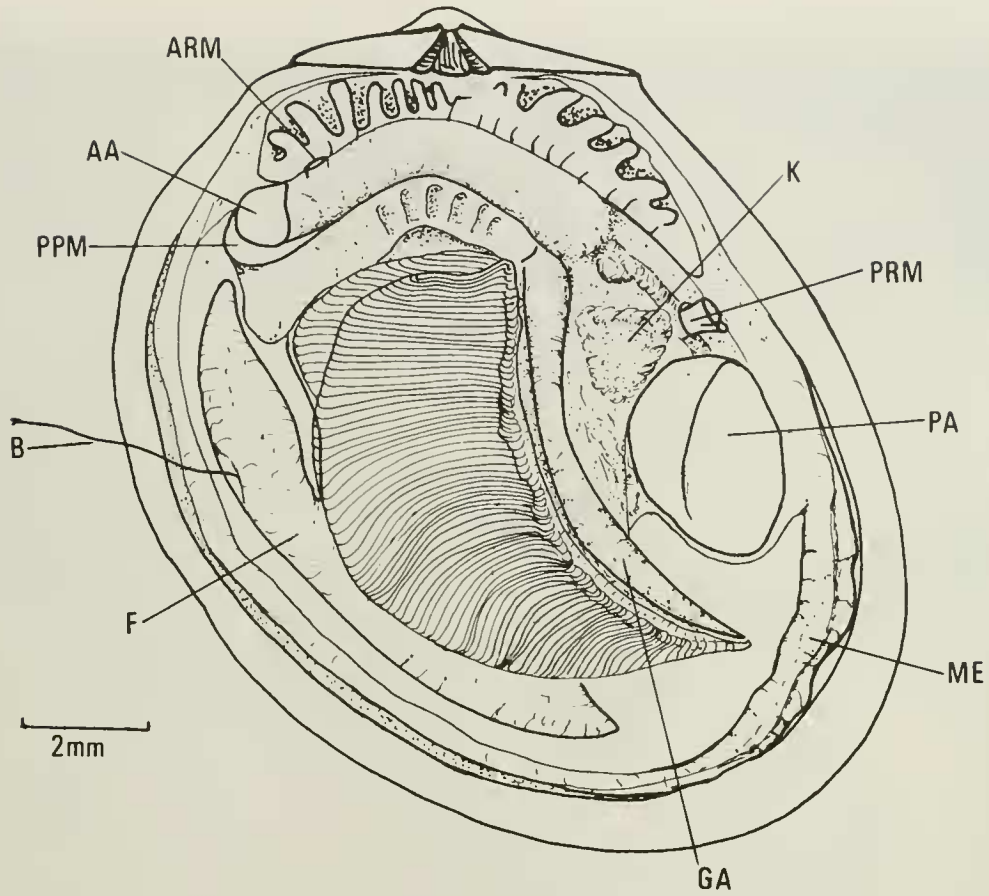
Juveniles have a concentric spicate periostracum, but the adults are more of the 'thatched' type.

Habitat: Sands and muds.

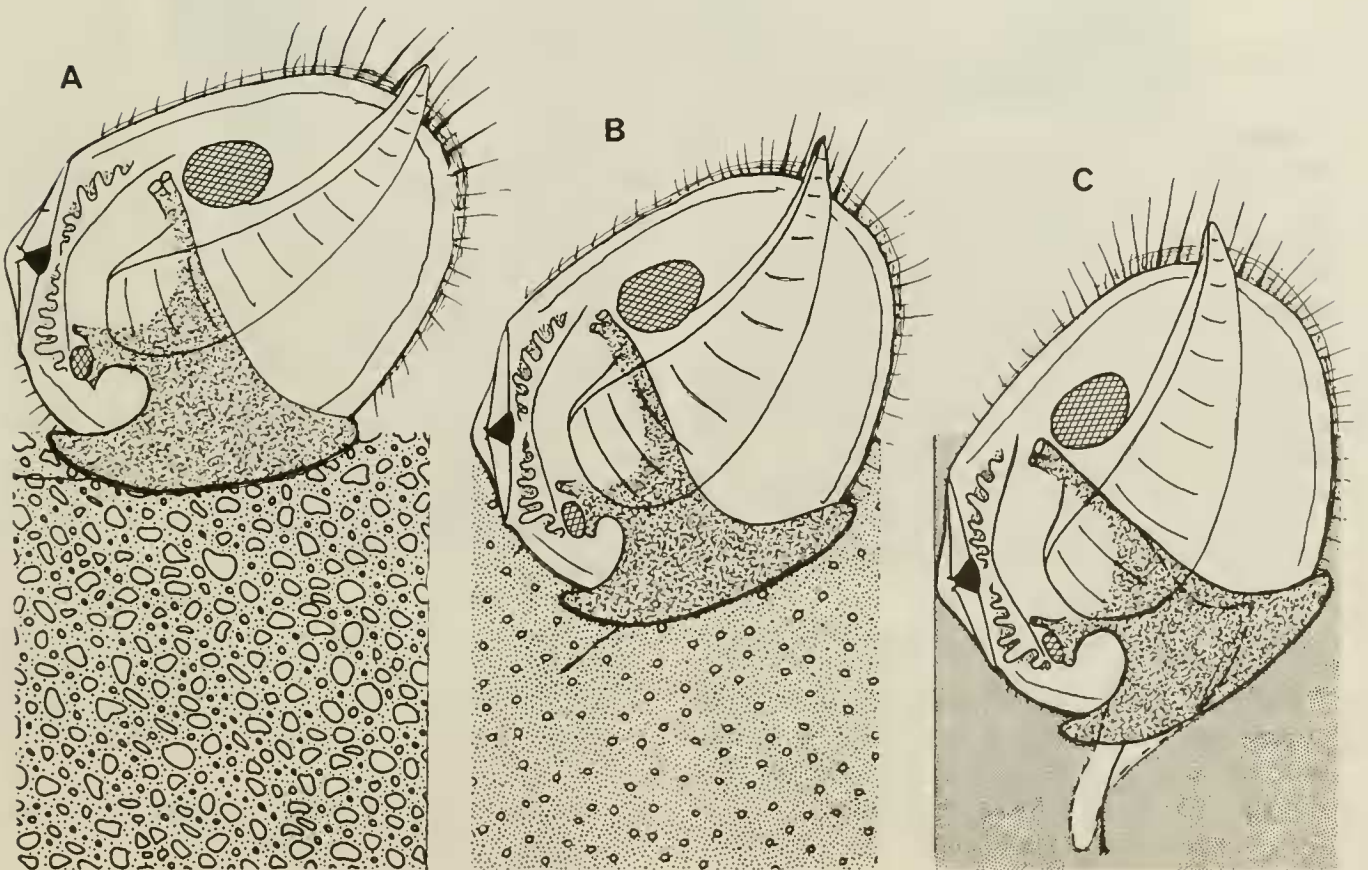
Bathymetric range: 100–2020 m.

Distribution: Japan.

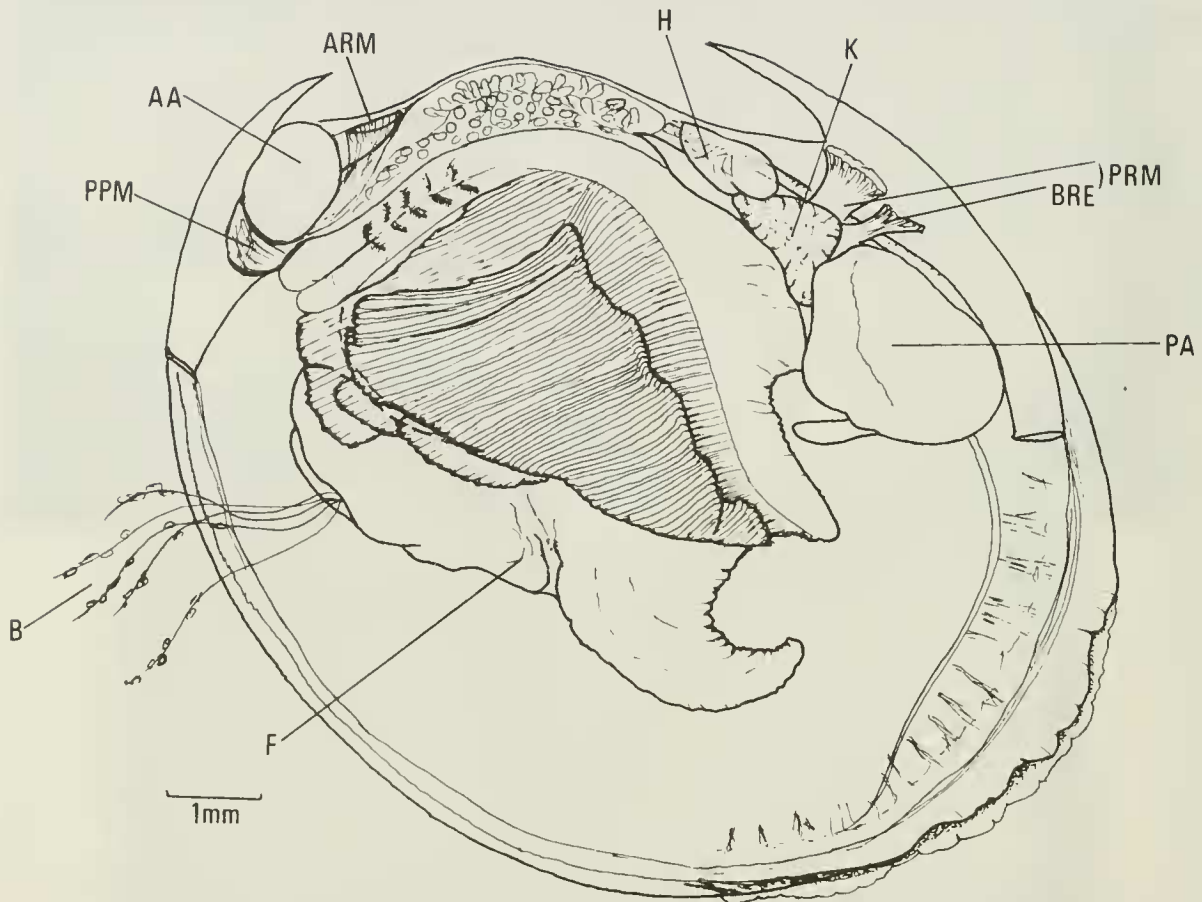




APP. FIG. 11. Gross anatomy of *Limopsis aurita* Brocchi (left mantle lobe removed).



APP. FIG. 12. Life positions of *Limopsis aurita* in A gravel, B sand and C mud.



APP. FIG. 13. Gross anatomy of *Limopsis diegensis* Dall (left mantle lobe removed). This anatomy is typical of all M.C. V forms.

#### Morphological Class VI

Diagnosis: Small species: diam. 6 mm. Relatively slightly tumid, inequilateral, becoming slightly obliquely oval. Sculpture weak. Periostracum pilose, of dense short stubby bristles, not fringing. Heteromyarian condition slight. Hinge moderately strong but consisting of few teeth. Ligament small, Type C. Inner margin crenulate and nodular. Anatomically similar to M.C. V, but showing a suite of abyssal adaptations (Oliver & Allen, 1980b). Byssus of 3–5 slender, long, fine threads.

Habitat: Ooze.

Bathymetric range: 3500–5500 m

Distribution: Atlantic Ocean.

Species complement: *Limopsis galathea* Knudsen, 1970.

Two abyssal Pacific species have shell similarities to *Limopsis galathea* but anatomical data are not available to substantiate this overall similarity. The species are *L. panamensis* Dall, 1908 and *L. juarezi* Dall, 1908.

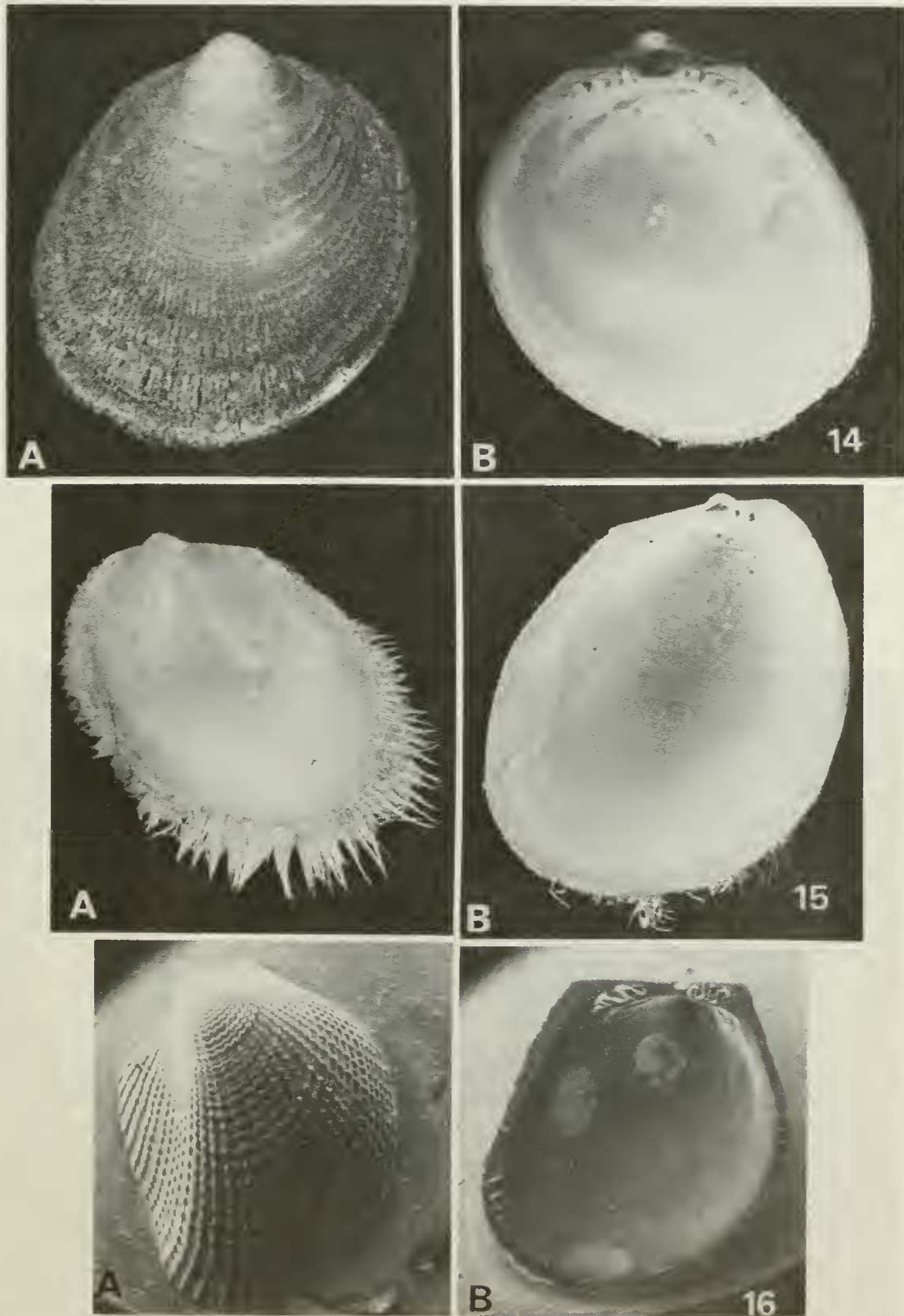
#### Morphological Class VII

Diagnosis: Small species reaching 15 mm diam. Relatively tumid, inequilateral, becoming markedly obliquely oval with a tendency to develop a short straight antero-dorsal margin. This development may not always occur. Shell relatively thick. Hinge reduced anteriorly, but teeth relatively large. Ligament Type A. Heteromyarian condition extreme, the minute anterior adductor with a prominent myophore. Inner margin crenulate, evenly nodular in juveniles, in adults reduced to 3–5 strong postero-ventral ridges. Anatomically similar to M.C. IV, but the byssus element of the posterior retractor is large and not attached to the shell but inserted into the posterior adductor. The toe of the foot is bulbous and the byssus gland is large. The byssus consists of a sheath with 4–6 short strap-like threads (App. Figs. 15 and 17).

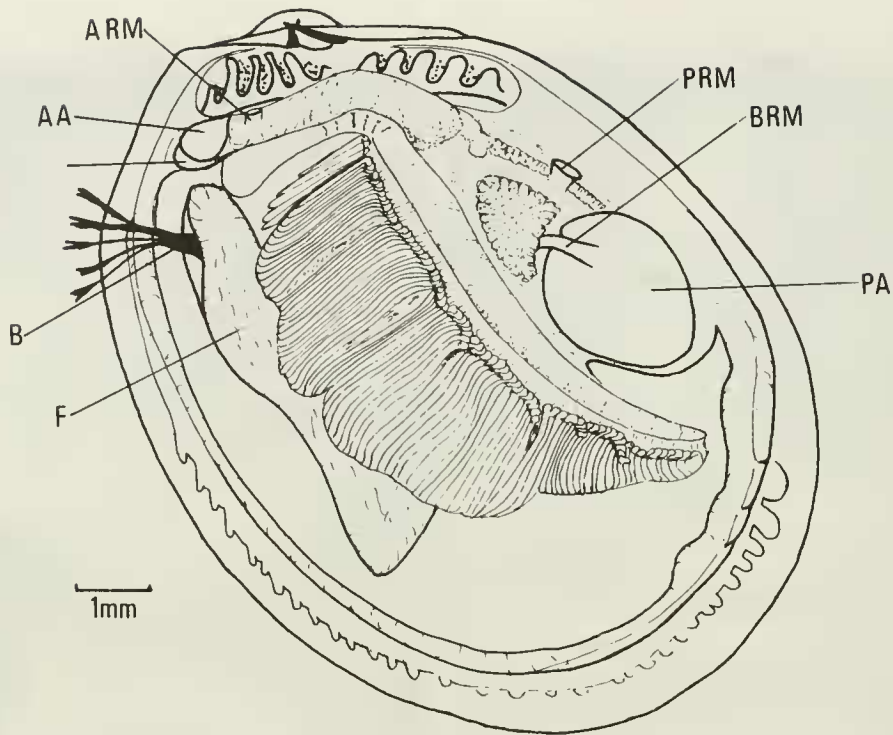
Habitat: Gravels, shell and coral hash, occasionally on finer sediments.

Bathymetric range: 50–2500 m.

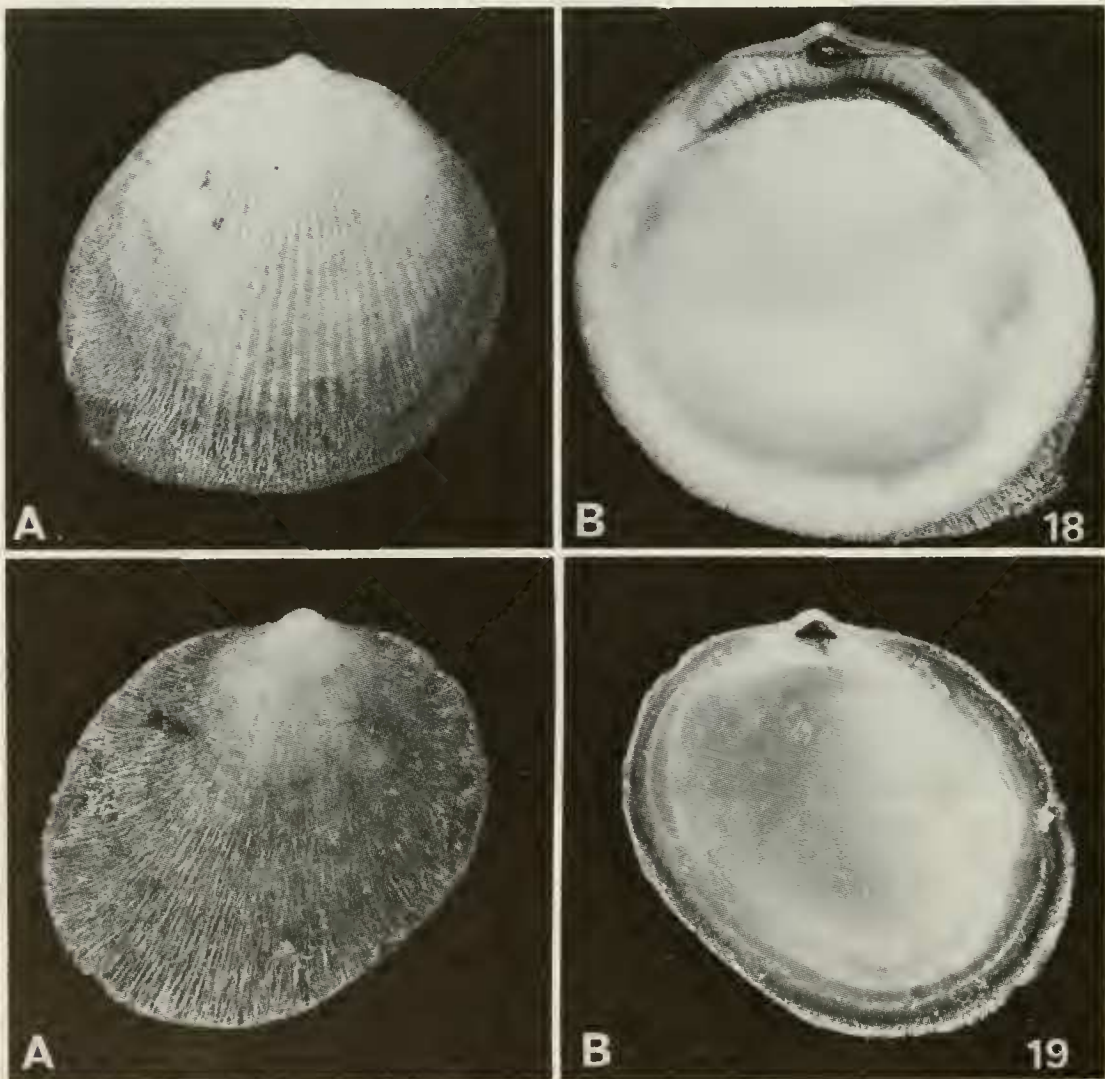




APP. FIG. 14. *Limopsis oblonga* A. Adams. Sagami Bay, Japan. RSM. Diam. 14 mm. APP. FIG. 15. *Limopsis minuta* Philippi. Bay of Biscay. MNHNP. Diam. 12 mm. APP. FIG. 16. *Limopsis natalis* Barnard. Off Natal. NM. Diam. 4 mm.

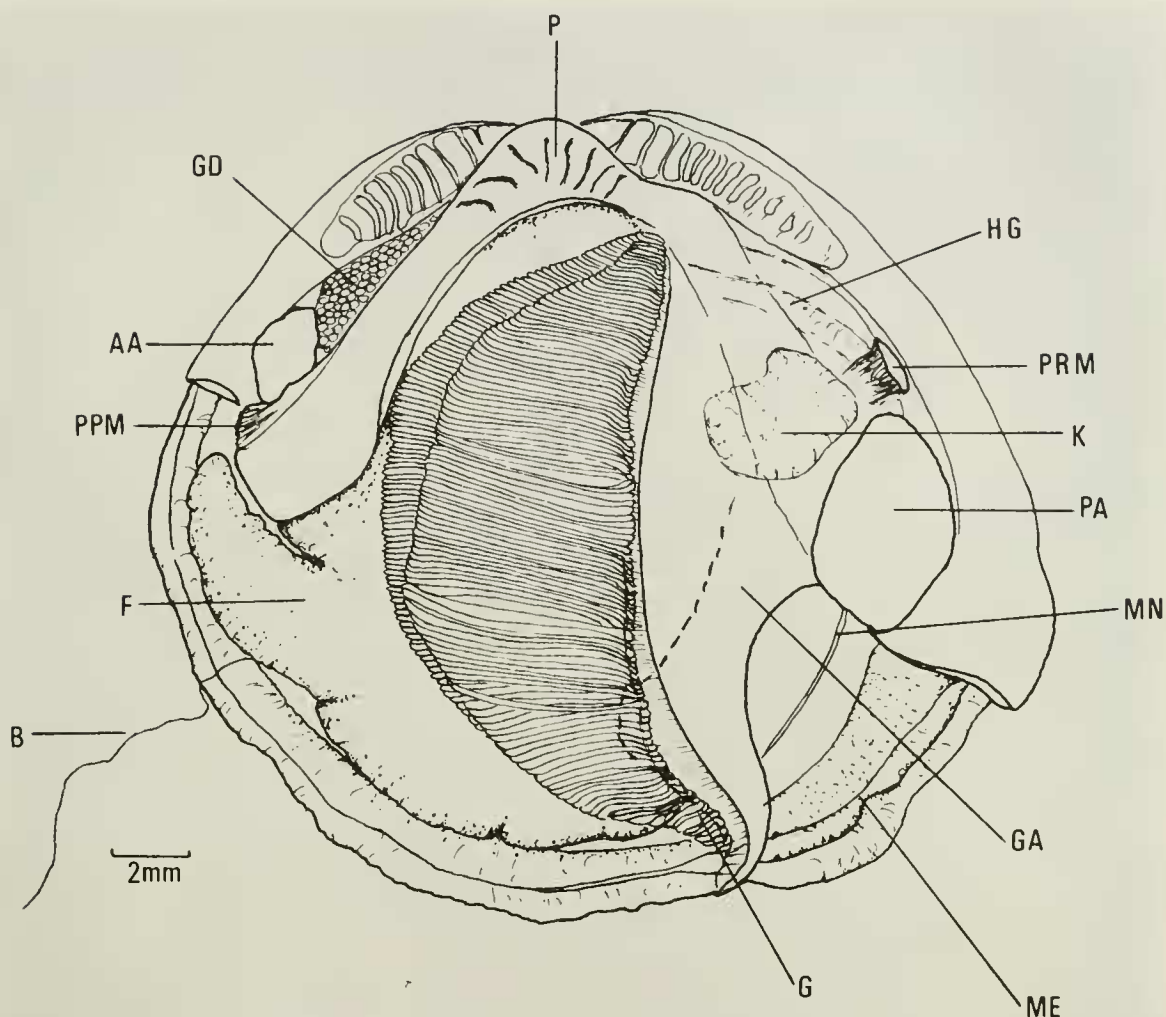


APP. FIG. 17. Gross anatomy of *Limopsis minuta* Philippi (left mantle lobe removed).



APP. FIG. 18. *Limopsis multistriata* (Forskål). Off Kenya. MCZ. Diam. 25 mm. APP. FIG. 19. *Limopsis bassi* Smith. South Australia. SAM. Diam. 25 mm.





APP. FIG. 20. Gross anatomy of *Limopsis multistriata* (left mantle lobe removed).

Distribution: Atlantic Ocean.

Species complement: *Limopsis minuta* (Philippi, 1836) and *L. abyssicola* A. Adams, 1862.

The New Zealand species *Limopsis lata* Smith, 1885 has a similar shell morphology but no confirmatory anatomical details are available.

#### Morphological Class VIII

Diagnosis: Minute species rarely exceeding diam. of 5 mm, relatively tumid, becoming obliquely quadrate with a long straight anterodorsal margin. Sculpture weakly decussate. Periostracum 'thatched.' Ligament small, Type C. Dorsal area small. Hinge reduced anteriorly with few but relatively large teeth. Heteromyarian condition extremely advanced. Anterior myophore small. Margin crenulated as in M.C. VII except that the postero-ventral emphasis is present in all but the smallest specimens. Anatomically similar to M.C. VII but there is no specialized byssus

retractor. Byssus consists of 3–5 short strap-like strands (App. Fig. 16).

Habitat: Sands and shell gravels.

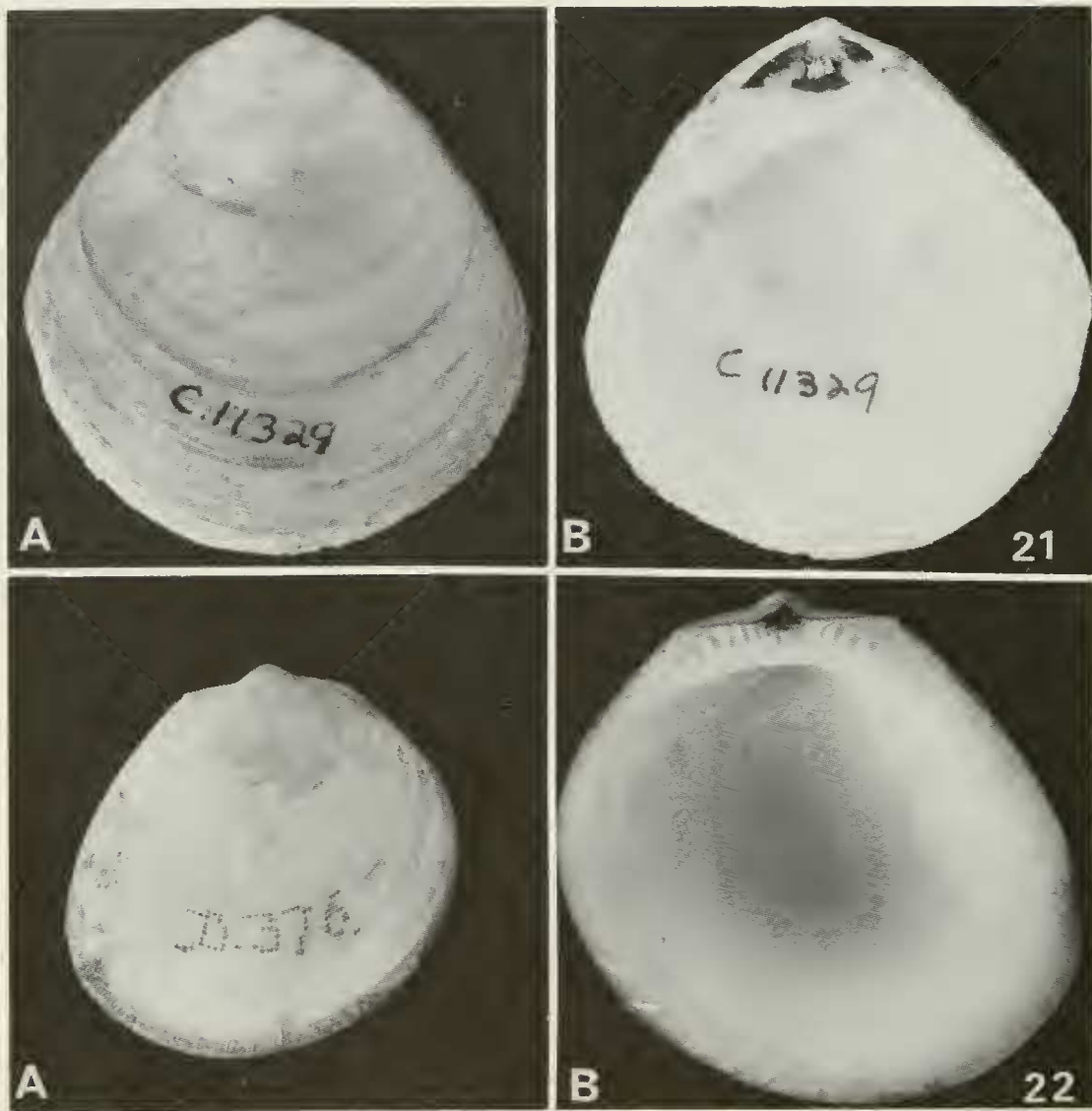
Bathymetric range: 100–600 m.

Distribution: Caribbean and Southeast Africa.

Species complement: *Limopsis antillensis* Dall, 1881; *L. natalis* Barnard, 1964 and *L. elachista* Sturany, 1899.

#### Morphological Class IX

Diagnosis: Moderately large species: diam. 25–45 mm. Equivalve, compressed, becoming obliquely circular, some large specimens dorsally attenuate. Shell thick. Sculpture of both concentric and radial ridges, more or less decussate in juveniles but radially ribbed in adults. Periostracum 'thatched,' but not persistent except at the postero-ventral margin. Dorsal area variable, usually small and narrow, but in dorsally attenuate species this area is expanded, remaining deeply cleft. Ligament Type A, variable and may be large.



APP. FIG. 21. *Limopsis loringi* Angas. Port Stephen, New South Wales. AMS. Diam. 33 mm. APP. FIG. 22. *Limopsis eucosmus* Verco. Gt. Australian Bight. SAM. Diam. 21 mm.

Hinge strong, teeth numerous, in two distinct series set on a high arch, central teeth of each set are the largest. Heteromyarian condition slight, both scars with fine buttresses. Shell between scars evenly radially striate. Inner margin crenulated, fluted. Foot with reduced toe and heel, blade-like, highly muscular. Posterior pedal retractors simple, large. Anterior dorsal retractors spread over the visceral mass with little or no shell attachment. Byssus gland small but capable of producing a single long fine thread which is, however, rarely observed. Gill axis orientated vertically relative to the hinge plate; axis musculature very small. Palps with numerous well-developed sorting ridges. Mantle edge greatly thickened postero-ventrally (App. Figs. 6B, 18 and 20).

Habitat: Sands, silts and muds.

Bathymetric range: 0–400 m.

Distribution: Indo-Pacific and South Australia.

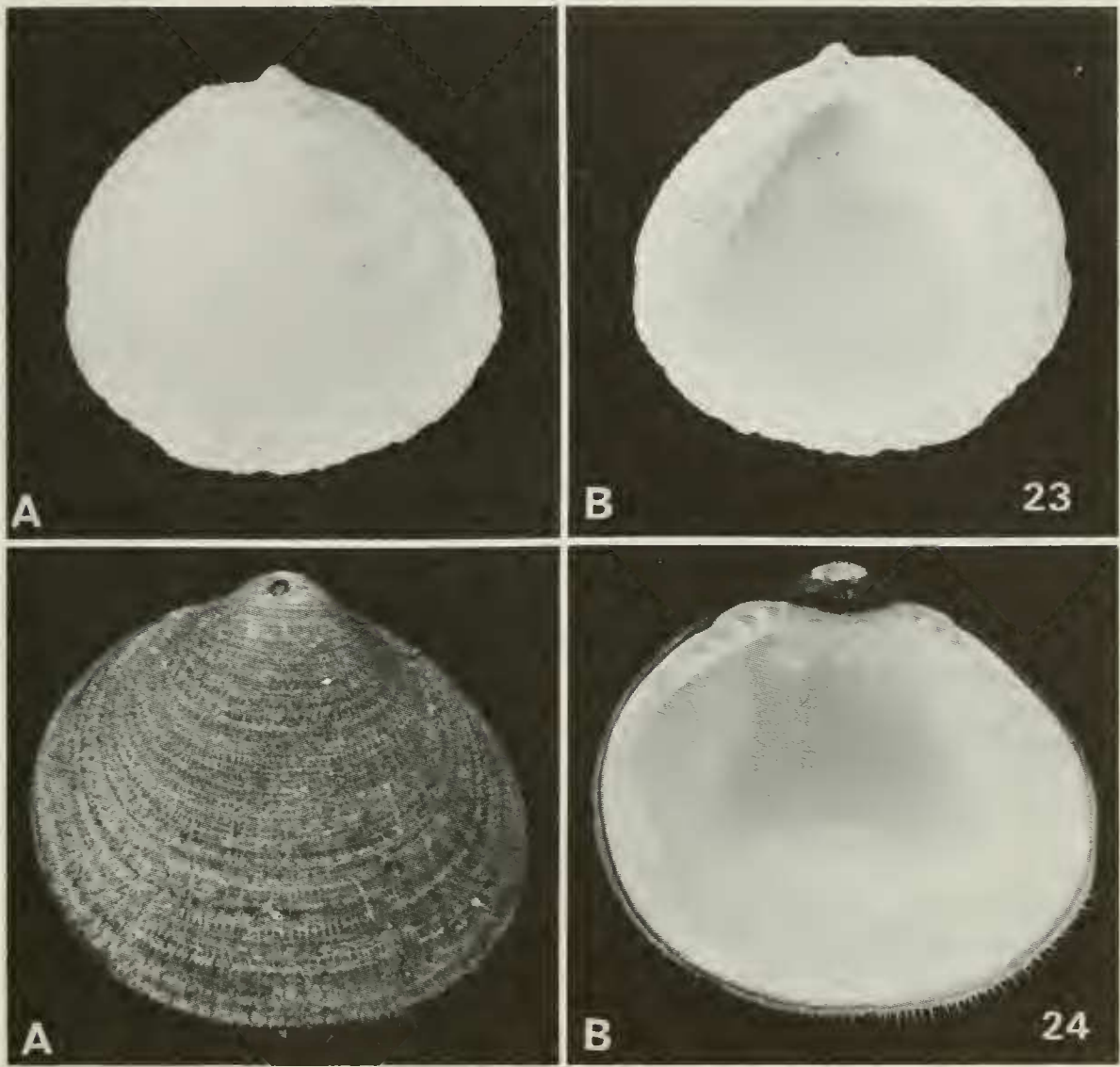
Species complement: *Limopsis multistriata* (Forskål, 1775); *L. compressa* G. & H. Nevill, 1874; *L. cancellata* (Reeve, 1843); *L. woodwardi* A. Adams, 1862; *L. macgillivrayi* A. Adams, 1862; *L. torresi* Smith, 1885; *L. japonica* A. Adams, 1862; *L. forskali* A. Adams, 1862; *L. soyoae* (Habe, 1953); *L. tenisoni* T. Woods, 1877; *L. tenuiradiata* Cotton, 1931; *L. forteradiata* Cotton, 1931.

Habits: J. D. Taylor (personal communication) has observed *Limopsis multistriata* living in sub-littoral sands off Shimoni, Kenya. They were observed to burrow completely in the sand although a number were lying free on the surface.

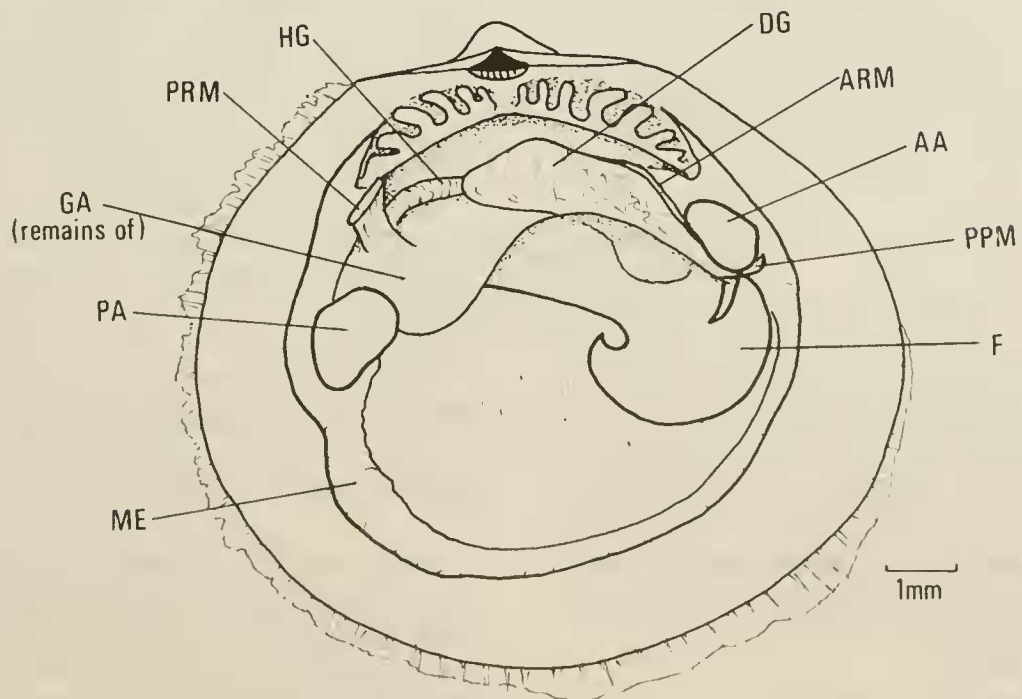
*Limopsis bassi* Smith, 1885

This species is similar to M.C. IX species, but is obliquely oval with a less rounded anterior margin. The sculpture is weaker, as is

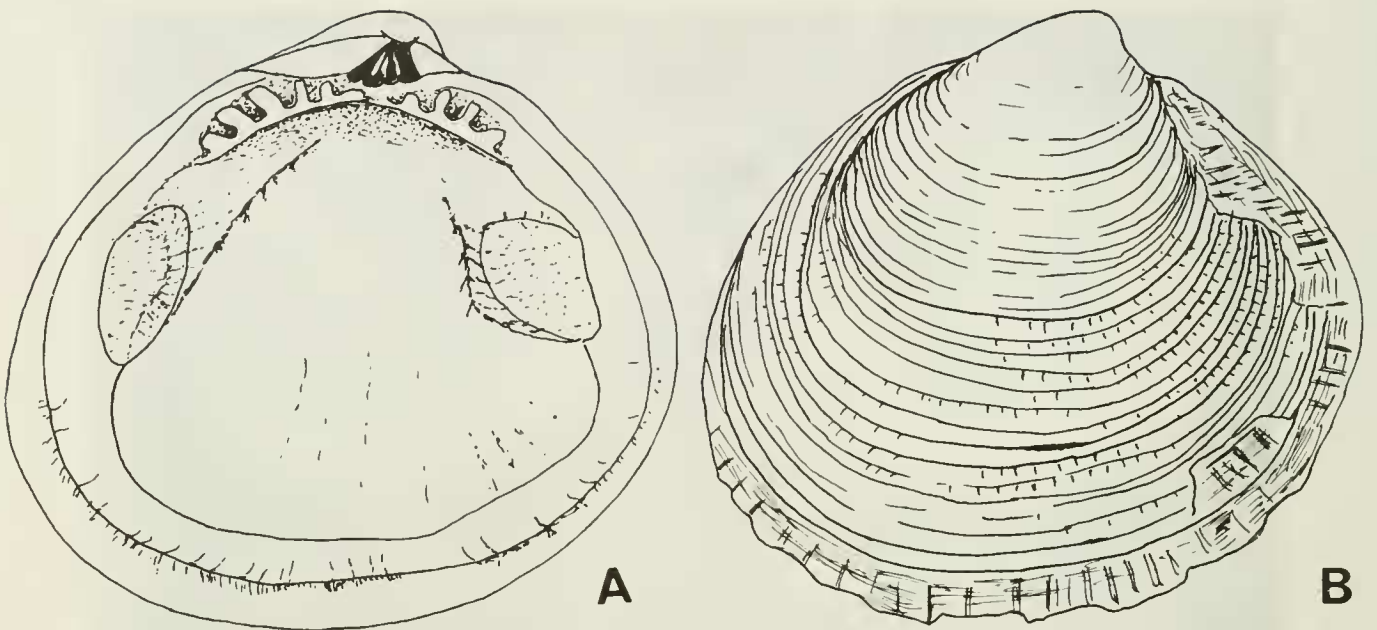




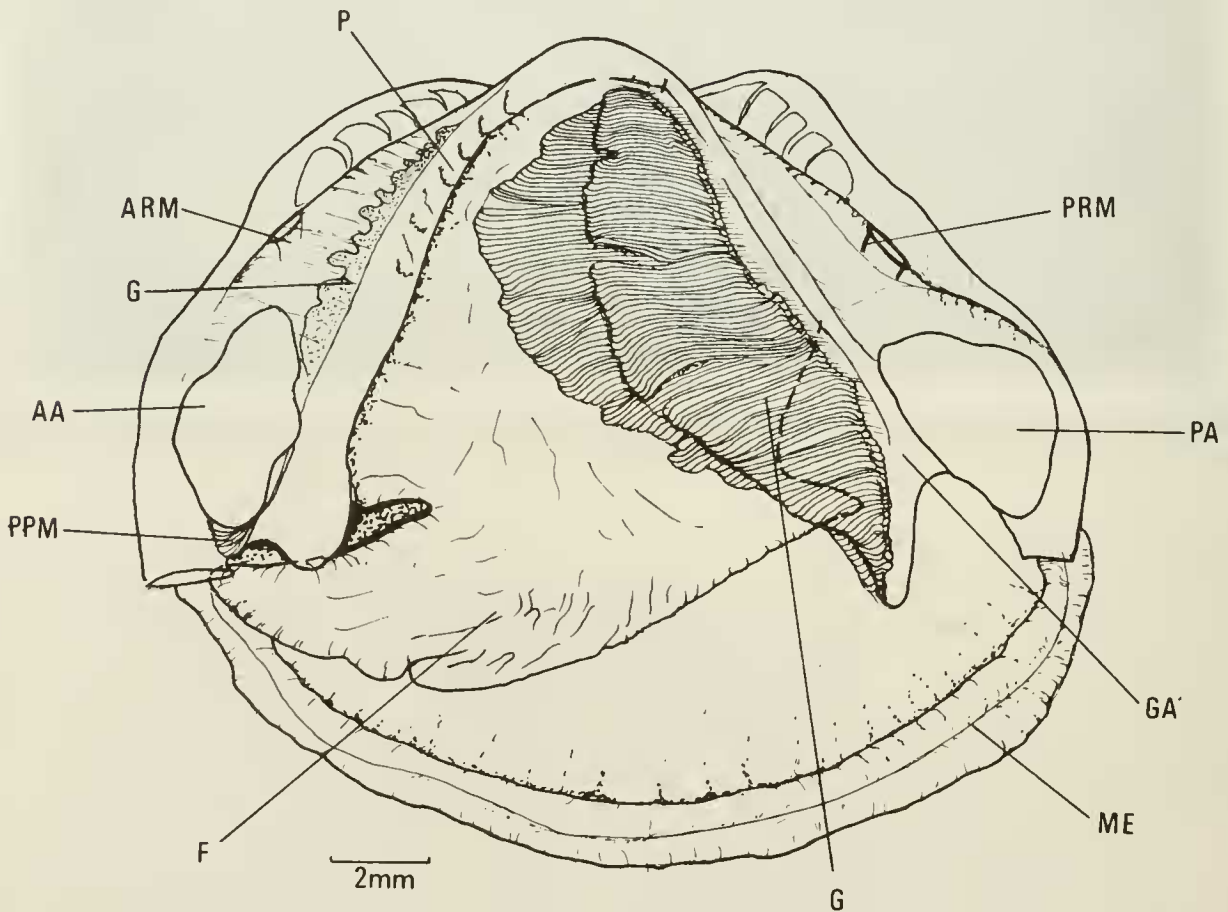
APP. FIG. 23. *Limopsis vixornata* Verco. Neptune Island. South Australia. SAM. Diam. 10 mm. APP. FIG. 24. *Limopsis lilliei* Smith. South Orkney Islands, Antarctica. NMW. Diam. 14 mm.



APP. FIG. 25. Gross anatomy of *Limopsis vixornata* Verco.



APP. FIG. 26. *Limopsis brazieri* Angas. Port Jackson, New South Wales. BMNH. Diam. 5 mm.



APP. FIG. 27. Gross anatomy of *Limopsis lilliei* Smith (left mantle lobe removed).

the hinge. The heteromyarian condition is greater, similar to that of M.C. I. The foot has a well-developed toe. The antero-dorsal retractors have shell attachments. The gill axis is orientated obliquely (App. Fig. 19).

Habitat: Sands.

Bathymetric range: Shelf zone.

Distribution: South Australia.

#### Morphological Class X

Diagnosis: Very similar to M.C. IX, but the sculpture is very finely decussate and the inner margin is smooth. Tevesz (1977) shows the anatomy to be similar to that of M.C. IX in the form of the foot and orientation of the gill axis. The byssus differs in being active, pro-



ducing up to five long fine threads (App. Fig. 21).

Habitat: Shell hash.

Bathymetric range: 40–70 m.

Distribution: Southeast Australia.

Species complement: *Limopsis loringi* Angas, 1873; *L. soboles* (Iredale, 1931) and *L. dannevigii* (Iredale, 1931).

Habits: Tevesz (1977) described the burrowing actions of *Limopsis loringi* and *L. soboles*. Burrowing action is slow, taking up to 45 mins to burrow completely up to the postero-ventral margin. No indication of ploughing activity was given by Tevesz.

*Limopsis eucosmus* Verco, 1907 (App. Fig. 22)

This is a South Australian species which is similar in outline and anatomy to *L. bassi*, i.e. it is a heteromyarian oblique form with a toed foot. Its other shell characters are, however, of the M.C. X form. The variety *penelevis* Verco, 1907 is even more extreme in its thinner shelled compressed form. The character of the byssus is not known; the byssus slit is well developed.

#### Morphological Class XI

Diagnosis: Small species reaching 12 mm in diam. Equivalve, compressed, almost inequilateral, sub-circular with a slight posterior extension, large specimens dorsally attenuate. Umbos very slightly prosogyre. Shell moderately thick. Sculpture concentric with very weak radial markings. Periostracum 'thatched' but not persistent. Dorsal area small, narrow. Ligament small, Type A. Hinge moderate, teeth in two series on a moderate arch, central teeth in each set dominant. Adductor scars sub-equal, heteromyarian condition slight, both scars weakly buttressed. Margin smooth. Examination of dried soft parts showed some critical features. Foot bladeli-like with small heel and toe. Posterior pedal retractors large. Anterior retractor with little or no shell attachment. The dried translucent foot showed no trace of the dark staining typical of the byssus gland. No byssus slit was observed. Mantle edge greatly thickened (App. Figs. 23 and 25).

Habitat: Unknown.

Bathymetric range: 70–200 m.

Distribution: South Australia.

Species complement: *Limopsis vixornata* Verco, 1907 and *L. occidentalis* Verco, 1907.

#### Morphological Class XII

Diagnosis: Small shells reaching 7 mm in diam. Equivalve, relatively slightly tumid, sub-equilateral with slight posterior extension, longer than high; sub-elliptical. Umbos prosogyre. Shell thick. Sculpture concentric with very weak radial markings. Dorsal area short, ligament relatively large Type A. Hinge moderately strong but with few teeth. Heteromyarian condition slight, adductor scars sub-equal, both buttressed. Margin smooth. No anatomical details available (App. Fig. 26).

Habitat: Unknown.

Bathymetric range: Shallow shelf zone.

Distribution: New South Wales, Australia.

Species complement: *Limopsis brazieri* Angas, 1871.

#### Morphological Class XIII

Diagnosis: Medium-sized species: diam. 20–25 mm. Equivalve, relatively slightly tumid, sub-equilateral, very slightly posteriorly extended, sub-elliptical. Shell thin. Sculpture finely decussate. Periostracum pilose, persistent. Hinge weak, teeth in two series on a low arch, ligament Type D. Adductor scars large, sub-equal, with very fine buttress lines. Internally striate. Margin smooth. Foot large, toe and heel not elongate, pedal retractors simple, posterior pair large. Byssus gland present but very small, no byssus observed. Gill axis orientated vertically with very little musculature. Mantle edge thickened, especially postero-ventrally (App. Figs. 6C, 24, and 27).

Habitat: Muds, muddy sand and muddy gravel mixtures.

Bathymetric range: 80–500 m.

Distribution: Antarctic Ocean.

Species complement: *Limopsis lillieii* Smith, 1885; *L. hirtella* Mabile & Rochebrune, 1889; *L. enderbyensis* Powell, 1958 and *L. scotiana* Dell, 1964.